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Although endothermy is one of the most significant evolutionary developments in the vertebrates, its origins among extinct taxa have traditionally been difficult to determine. Endothermy is primarily an attribute of the "soft anatomy," and its key features, such as complex lungs, elevated blood oxygen carrying capacity and mitochondrial density, do not fossilize. Previously, only one preservable morphological feature, the presence of complex nasal turbinates, has, anecdotally, been considered very suggestive of endothermy in the ancestry of mammals.

This thesis examines the functions of the nasal turbinates of extant mammals with respect to physiological characteristics of endothermy. The fossil record of nasal turbinates is also studied. Nasal turbinates serve two distinct functions: olfaction and conditioning of respiratory air. The respiratory turbinates have previously

been found to reduce respiratory water loss in desert mammals. Experimental data presented here indicate that these structures also substantially reduce respiratory water loss in non-desert mammals. These data support the conclusion that respiratory turbinates represent an adaptation to reduce desiccation associated with high pulmonary ventilation rates, and may have evolved in association with the origin of elevated ventilation rates and endothermy. Conversely, no particular correlation with endothermy exists for the olfactory turbinates.

In extant mammals, the nasal turbinates attach to ridges along the lateral walls of the nasal cavity, which present a characteristic pattern. Studies of similar ridges in the nasal cavities of the ancient mammals and their ancestors, the mammal-like reptiles (Therapsida), indicate that respiratory turbinals first appear in two groups of advanced therapsids, Therocephalia and Cynodontia. This suggests that the evolution of "mammalian" oxygen consumption rates may have begun as early as the Late Permian, 260 million years ago, and developed largely independently in therocephalians and cynodonts. Full mammalian endothermy may have taken as much as 40 to 50 million years to develop.

NASAL TURBINATES AND THE EVOLUTION OF MAMMALIAN ENDOTHERMY

by

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CHAPTER 1

GENERAL INTRODUCTION

Endothermy, or "warm-bloodedness," is one of the major evolutionary developments of vertebrates, and among the most significant features that distinguish extant mammals and birds from reptiles and other vertebrates (Bennett and Dawson 1976; Bennett and Ruben 1979, 1986; Bennett 1991). High rates of internal heat production which are the hallmark of endothermy, enable birds and mammals to maintain a high and stable body temperature over a wide range of ambient temperatures (Schmidt-Nielsen 1990). As a result, these animals are able to thrive in environments with cold or highly variable thermal conditions, and in nocturnal niches generally unavailable to vertebrate ectotherms (Willson 1984).

The increased aerobic capacity associated with endothermy allows these animals to sustain activity levels well beyond the capabilities of ectotherms (Bennett and Dawson 1976; Bennett and Ruben 1979; Bennett 1982, 1991). Ectotherms, such as reptiles, typically rely on non-sustainable, anaerobic metabolism for all activity beyond relatively slow movements (Bennett and Dawson 1976; Bennett 1991). Although they are capable of bursts of intense exercise, they rapidly fatigue as a result of lactic acid accumulation (Ruben 1989; Bennett 1991). Endotherms,

conversely, are able to sustain even relatively high levels of activity for extended periods of time, which has considerable ecological advantages. Such stamina enables these animals to forage over large territories, for example, and to perform extensive seasonal migrations in pursuit of favourable resource conditions. The capacity of bats and birds to sustain powered flight is far beyond the aerobic capabilities of modern ectotherms (Bennett and Ruben 1979; Bennett 1991; Ruben 1991).

These factors, stamina and thermal independence, appear largely responsible for the present success of mammals and birds in the terrestrial and sub-aerial environments (Bennett and Ruben 1979; 1986; Willson 1984; Romer and Parsons 1986). Consequently, it is not surprising that the evolution of endothermy has received considerable attention (e.g., Hopson 1973; McNab 1978, 1983; Crompton et al. 1978; Bennett and Ruben 1979; Dawson and Grant 1980; Hulbert 1980, 1987; Taylor 1980; Else and Hulbert 1981, 1985; Bennett 1991; Ruben 1991). In addition, during the last two decades there has been considerable speculation, and much spirited debate, about the possible presence of endothermy in certain extinct reptilian lineages, such as dinosaurs and pterosaurs, which dominated the terrestrial and sub-aerial environments for most of the Mesozoic Era (e.g., Bakker 1971, 1972, 1975, 1986; De Ricqles 1974, 1976; Desmond 1975; Padian 1983; Paul 1988).

Unfortunately, despite its significance in vertebrate biology, endothermy has been very difficult to demonstrate in extinct forms, and the debate about dinosaur physiology, in particular, has been heated (see Thomas and Olson 1980; Bennett and Ruben 1986; Czerkas and Olson 1987). Endothermy is primarily an attribute of the "soft anatomy," which leaves a very poor fossil record. Physiologically, endothermy is achieved through prodigious rates of cellular oxygen consumption: mammalian resting metabolic rates are typically about 10x greater than reptilian rates (Bennett 1973; Else and Hulbert 1981), and avian rates are still greater, up to 15x reptilian rates (Schmidt-Nielsen 1984). To support such high respiration rates, endotherms have made profound structural and functional modifications to facilitate oxygen uptake, transport and delivery. Both mammals and birds have greatly increased pulmonary capacity and ventilation rates (Bennett 1973; Bernstein and Schmidt-Nielsen 1974; Perry 1983; Ruben et al. 1987; Piiper 1989), fully segregated pulmonary and systemic circulations and expanded cardiac output (Romer and Parsons 1986; Bennett 1991). They also have greatly increased blood volume and blood oxygen carrying capacities (Bennett 1973; Schmidt-Nielsen 1990), as well as increased mitochondrial density and enzymatic activities (Else and Hulbert 1981, 1985). Unfortunately, however, these key features of endothermic physiology are not preserved in fossils, mammalian, avian or otherwise.

Consequently, previous speculations concerning the possible presence of endothermy in extinct vertebrates have relied primarily on circumstancial evidence, such as predator-prey ratios (e.g., Bakker 1972, 1975), paleoclimatological inferences (e.g., Bakker 1975; Paul 1988), or on correlations with mammalian or avian morphology, such as posture (e.g., Heath 1968; Bakker 1971, 1972; Carrier 1987) and bone histology (e.g., De Ricqles 1974, 1976; Bakker 1975). Recently, however, Bennett and Ruben (1986) determined that most of these arguments are equivocal. Furthermore, the majority of the morphological arguments used previously are based predominantly on similarities to the mammalian (or avian) condition, without a clear functional correlation to endothermic processes per se. Very few empirical studies are available which describe an unambiguous, and exclusive, functional relationship to endothermy, of a preservable morphological characteristic. It is precisely the purpose of this thesis to provide such a study.

Bennett and Ruben (1986) concluded that there was only one morphological feature very suggestive of endothermy in the ancestry of mammals - nasal turbinates. These are thin, complex structures in the mammalian (and avian) nasal cavity, but are not present in any ectothermic vertebrate. Their function has been described in certain desert mammals, where they are associated with conditioning respired air and with reduction of respiratory water loss, in addition to an

olfactory function (Jackson and Schmidt-Nielsen 1964; Collins et al. 1970). Previously, the respiratory turbinates were regarded principally as an adaptation to desert conditions (e.g., Schmidt-Nielsen 1969, 1981). However, complex nasal turbinates are found throughout mammals, and do not differ markedly in complexity between desert and non-desert mammals (e.g., Negus 1958). It seems therefore likely that nasal turbinates may have a more general and fundamental relationship to mammalian respiratory physiology.

In this thesis, I have addressed two main problems. The first is physiological, and concerns the functions of the mammalian nasal turbinates. The second is paleontological, and deals with the fossil record of nasal turbinates in mammals and their ancestors, the mammal-like reptiles.

In Chapter 2, I examine the function of the nasal turbinates of non-desert mammals, and attempt to elucidate their role in reducing respiratory water loss with respect to characteristics of mammalian respiratory physiology. Ectothermic and endothermic respiratory characteristics are also compared. After a distinction is made between olfactory and respiratory turbinals, I conclude that the respiratory turbinals of mammals most likely represent an adaptation to high pulmonary ventilation rates, a key aspect of mammalian endothermy, and probably evolved in concert with the development of endothermy.

In Chapter 3, I review the functional distinction between the various types of turbinates, as well as their preservation in the fossil record. The paleontological record of nasal turbinates of mammals and mammal-like reptiles is studied. Newly prepared fossil material is described, which suggests that respiratory turbinals appeared as early as the Late Permian, about 260 million years ago. This suggests that "mammalian" metabolic rates may have taken some 40 to 50 million years to develop fully, until the Late Triassic, when the first mammals appeared, about 215 million years ago.

CHAPTER 2

THE EVOLUTION OF NASAL TURBINATES AND MAMMALIAN ENDOTHERMY

by

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Abstract

Complex nasal turbinal bones are associated with reduction of respiratory water loss (RWL) in desert mammals, and have previously been described as an adaptation to xeric conditions. However, complex turbinates are found in virtually all mammals. Experimental data presented here indicate that turbinates also substantially reduce RWL in five species of small mammals from relatively mesic environments. The data support the conclusion that turbinates did not evolve primarily as an adaptation to particular environmental conditions, but in relation to high ventilation rates, typical of all mammals. Complex turbinates appear to be an ancient attribute of mammals, and may have originated among the therapsid ancestors of mammals, in relation to elevated ventilation rates and the evolution of endothermy.

Introduction

One of the most distinctive of mammalian features is the presence in the nasal cavity of a series of thin, often highly convoluted sheets of bone, the turbinals (Figs. 1, 2). Named after the bones on which they insert, there are usually several ethmoturbinals, a nasoturbinal and a maxilloturbinal in each nasal passage. These chondrocranial elements ossify from the ethmoid cartilage and the nasal capsules (Moore 1981).

The naso- and ethmoturbinals are located in the dorsal and posterior portions of the nasal passages, dividing this region into a series of blind recesses. They are often partially protected from respiratory air currents by a transverse lamina (Fig. 1). These turbinals bear primarily olfactory (sensory) epithelium, and serve to greatly increase the surface area of these tissues (Negus 1958; Moore 1981; Romer and Parsons 1986).

The maxilloturbinals, on the other hand, are covered with a non-olfactory, respiratory mucosa. They are situated directly in the line of respiratory air flow, in the antero-ventral portion of the nasal cavity (Fig. 1), and are typically complex structures, consisting of elaborately scrolled, folded or finely branched lamellae (Fig. 2). These maxilloturbinals, or "turbinates," are usually described as having an air-conditioning function: inhaled air is filtered, warmed to body temperature and humidified

by evaporation of water from the turbinal mucosa, prior to reaching the lungs (Negus 1958; Walker et al. 1961; Romer and Parsons 1986). Although important, this may not be the primary function of complex turbinates. For example, in humans, which have very reduced turbinates (Fig. 2), inhaled air is still almost fully conditioned when it reaches the trachea (Cole 1953; Ingelstedt 1956; Proctor et al. 1977; Guyton 1991).

The maxilloturbinals are also associated with reduction of respiratory water loss in several mammals from arid and semi-arid environments, including the kangaroo rat, Dipodomys, and several desert ungulates, such as camels and giraffes (e.g. Jackson and Schmidt-Nielsen 1964; Schmidt-Nielsen 1969, 1972a, 1972b; Collins et al. 1971; MacMillen 1972; Langman et al. 1978, 1979; Schmidt-Nielsen et al. 1981; Schroter et al. 1987; Schroter et al. 1989). In these animals, the convoluted structure of the turbinates facilitates a countercurrent exchange of heat and water between respired air and turbinal lining. Evaporation of moisture, which humidifies inhaled air, also cools the turbinal mucosa, and creates a thermal gradient along the turbinates. Upon exhalation, warm expired air, saturated with water, is cooled when it again passes through these structures. As a result, "excess" water condenses on the epithelial surface, and is recycled during the next inspiration. In short, reduction of respiratory water loss occurs because air is exhaled below core body temperature,

allowing water to be recovered rather than lost to the environment (Walker et al. 1961; Jackson and Schmidt-Nielsen 1964; Collins et al. 1971; Schmidt-Nielsen 1972a, 1972b). Alternately, in humans the ability to cool expired air, although present, is relatively limited (Cole 1953; Schmidt-Nielsen et al. 1970b).

Reducing water loss is of particular importance to animals from xeric environments, and complex, water-recovering turbinates are often presented as an example of adaptation to arid conditions (eg. Schmidt-Nielsen, 1969, 1972a, 1972b, 1981; Schmidt-Nielsen et al. 1981; Langman et al. 1979; Langman 1985). However, this explanation fails to address the presence of remarkably complex and extensive turbinates in nearly all mammals. There are variations in their configuration and complexity (see Fig. 2), but these appear to be correlated with phylogenetic grouping rather than environment (Negus 1958; Moore 1981). For example, artiodactyls, including both camels and water buffalo, typically have large, loosely scrolled turbinates, while those of most carnivores are usually more compact, intricately branched structures (Negus 1958: pp 200-201; Schmidt-Nielsen et al. 1981). Only certain specialized groups, such as cetaceans and many primates, have reduced turbinates. In general, the turbinates of almost all mammals are far more complex than those of other vertebrates (Negus 1958; Moore 1981; Romer and Parsons 1986).

Complex turbinates are unknown in reptiles, many of which live in desert environments. They are absent altogether in turtles (Romer and Parsons 1986), while in lizards and snakes there is only a single, partially convoluted concha, covered with olfactory epithelium and situated outside the main respiratory air flow (Negus 1958; Romer and Parsons 1986). In crocodilians three simple conchae are present, at least partially covered by olfactory epithelium (Parsons 1967). However, in a number of birds the turbinals approach mammalian complexity and organization (Negus 1958; Bang 1961, 1964, 1966, 1968; Schmidt-Nielsen et al. 1970b; Murrish 1973).

The functional effect of complex turbinates, i.e. cooling of the nasal passages and expired air below core body temperature, has also been documented in many mammals from non-desert environments (cf. Table 1). Recent findings by Schroter and Watkins (1989) imply that a counter-current exchange of heat and water is possible in the nasal passages of non-desert as well as desert mammals. These observations suggest that complex turbinates might function to reduce respiratory water loss in mammals from many environments, and could be of more profound significance than merely an adaptation to arid conditions.

Additionally, the fact that complex turbinates are found in all mammalian subclasses (Negus 1958; Moore 1981) suggests that they evolved early in mammalian history, and may be a fundamental attribute of this class. This is

corroborated by indications of their presence in the earliest known mammals (Kermack et al. 1981), and possibly even among advanced mammal-like reptiles (Therapsida) (eg. Watson 1913; Brink 1956; Kemp 1982).

In this study, the association between complex turbinates and mammalian respiratory physiology is investigated. The effect of the turbinate complex on respiratory water loss is examined in several small mammals from relatively mesic environments, by comparing normal, nasopharyngeal breathing to oral breathing, when use of the turbinates is precluded. Rates of respiratory water loss of mammals and reptiles are also compared, and an explanation is presented for the evolution of the turbinate complex as an essential attribute of mammalian respiratory physiology.

Materials and Methods

Animal sources and maintenance

Experimental animals included rats (Rodentia, Muridae: Rattus norvegicus, Sprague-Dawley strain), ground squirrels (Rodentia, Sciuridae: Spermophilus beecheyi), ferrets (Carnivora, Mustelidae: Mustela putorius furo), rabbits (Lagomorpha, Leporidae: Oryctolagus cuniculus) and opossums (Marsupialia, Didelphidae: Didelphis virginiana). Rattus and Oryctolagus were obtained through Laboratory Animal Resources at Oregon State University, Mustela from local breeders and pet stores. Spermophilus were live-trapped at E.E. Wilson Wildlife Management Area, Benton County, Or. Didelphis were live-trapped in Corvallis, Benton Co., Or. All animals were adults, as judged by size. For reasons explained below, only female Mustela and male Didelphis were used.

Animals were maintained in captivity for approximately ten days. Rattus were kept in acrylic and metal-screen cages, five per cage, and fed Wayne Rodent Blox. Other taxa were kept in individual, metal cages. Spermophilus were fed Rodent Blox, Mustela were fed Purina high-protein dry kitten food. Didelphis were fed a mixture of dry dog and cat foods, and Oryctolagus were fed OSU rabbit diet. Food and water were provided ad libitum. Animals were maintained on

a 12L : 12D photoperiod, at approx. 18 ± 2°C. Animals were fasted for 12 h prior to testing.

Experimental Procedures.

To assess the effect of the turbinate complex on respiratory water loss, normal, nasopharyngeal breathing was compared to oral breathing, during which use of the turbinates was precluded by blockage of the external nares. Although perhaps not entirely comparable, oral breathing approximates nasopharyngeal breathing without a turbinate heat exchange system. Blockage of the external nares is far less injurious than surgical ablation of turbinates, and less likely to result in aberrant data. For each condition, total evaporative water loss was measured and standardized against oxygen consumption. Relative portions of the cutaneous and respiratory components were then estimated.

Three treatments were used: "control" (C), monitoring normal nasopharyngeal breathing; "experimental" (E), in which the external nares were closed; "anaesthesia-control" (A), decribed below. In Rattus, closure of the external nares was achieved by insertion of cotton plugs, followed by sealing the nostrils with cyanoacrylate cement. In the other taxa, the nares were sutured shut with #000 braided silk before sealing with cyanoacrylate cement. Plugs and sutures were applied under brief ether anaesthesia. Animals

recovered quickly from anaesthesia, and the plugs appeared to cause only minor discomfort to experimental animals. Following data collection, nasal plugs were checked for leaks, then removed. Animals appeared to have recovered almost immediately from the procedure.

Anaesthesia-control (A) treatments consisted of ether anaesthesia without plugging the nares. In some cases, data from "experimental" trials in which plugs had failed were used as control values.

Individual Didelphis and Oryctolagus were subjected to all three treatments. Rattus and Spermophilus were divided into two groups, measured either under C and E, or under C and A conditions. Individual Mustela were subjected to C and A, C and E, or all three treatments. Each individual animal was given at least one day to recover between treatments.

Oxygen consumption and evaporative water loss were measured simultaneously using open-circuit respirometry. Individual animals were placed in a plexiglass metabolic chamber (50 x 30 x 15 cm for rats, ground squirrels and ferrets, and 70 x 50 x 50 cm for opossums and rabbits) which contained a false bottom of metal wire screen over a reservoir of vegetable oil, to trap urine and feces. Data from experiments contaminated by urine or feces were discarded. Chamber temperature was regulated at 15.0 $\pm$ 2.0^{o}C to represent realistic environmental temperatures without causing undue cold or heat stress. Air flowing into

the chamber was passed first through columns of Drierite and Ascarite to absorb water and CO_2. Flow rates were monitored with Manostat flowmeters (calibrated to $\pm$ 1% accuracy). Varied flow rates were used for each species (cf. Table 2).

Animals were placed in the chamber at least 4 h prior to data collection to allow chamber equilibration (Lasiewski et al. 1966). Typically, animals were resting quietly after this period.

Oxygen content and relative humidity of efflux air were measured every 60 s for 55-90 min. Efflux air temperature was measured every 8 minutes, and was assumed to vary linearly between measurements. Relative humidity and air temperature were measured with an Extech 5070C solid state hygrometer (accuracy $\pm$ 3%) positioned in-line of the efflux air, immediately outside the metabolic chamber. This instrument was calibrated daily against a saturated NaCl solution (RH = 75%). The temperature function was calibrated to $\pm$ 0.1^{o}C with a thermometer traceable to the US Bureau of Standards. Following these measurements, efflux air was again led through Drierite and Ascarite, and fractional oxygen concentration was measured with a Beckman Model E2 paramagnetic oxygen analyzer. Oxygen consumption ($\dot{V}O_2$) was calculated according to steady state equations (Depocas and Hart 1957) and corrected to STP. Evaporative water loss (EWL) was calculated from RH and T_a data (Lasiewski et al. 1966), after correction for RH within empty chambers under identical conditions.

Measurements were performed during the resting phase of the animals' daily cycles. Data from active animals were excluded from calculations. Because male Mustela were constantly active, only data from females of this species were used. Female Mustela were frequently inactive for only a few periods of 10 - 20 min each in several hours of measurements. Therefore, to facilitate consistent comparisons between species and treatments, only the five lowest consecutive values of the $EWL/\dot{V}O_2$ ratio for each individual animal were used for analysis.

During the period in which Didelphis were investigated (spring and summer), females commonly carried pouch young. Data from animals in this condition did not represent single individuals, and female Didelphis were not used.

Nasal temperatures of control animals were measured at the external nares using a thermocouple thermometer (Cole-Parmer model 8500 - 40) and a Copper-Constantan probe (dia. 0.8 mm). This instrument was regularly calibrated to $\pm$ $0.1^{o}C$ against a thermometer traceable to the U.S Bureau of Standards. Animals were unrestrained or were held by hand (except Spermophilus, which were lightly anaesthetized with methoxyflurane). The thermoprobe was inserted to just inside the nasal opening (1 mm for the smaller animals, and 2-3 mm for the Oryctolagus and Didelphis), against the wall of the nasal passage, immediately after ambient temperature was measured. It was not possible to hold the probe in the airstream without touching the walls. These measurements

are comparable to the nasal temperatures presented by Getz (1968), Schmid (1976), Hill (1978) and others, and approximate the actual exhaled air temperature (Collins et al. 1971).

The respiratory (RWL) portion of evaporative water loss for control treatments was estimated for each species using minute volume estimates (after Stahl 1967, scaled for observed $\dot{V}O_2$) and water saturation density (CRC Handbook of Chemistry and Physics, 62nd Ed.) at observed nasal temperatures. The difference between this estimate and observed evaporative water loss represents cutaneous water loss. Cutaneous water loss was assumed to be similar in all treatments, and was subtracted from observed experimental EWL to obtain an estimate for respiratory water loss for animals in this condition.

Data presented are means $\pm$ SE. Means were compared using appropriate t-tests, or Mann-Whitney U-tests when sample variances were unequal. Statistical significance was accepted at $P < 0.05$.

Results

Observed rates of oxygen consumption ($\dot{V}O_2$) and evaporative water loss (EWL) are presented in Table 2. In all species, experimental treatment resulted in significantly greater water loss than control treatment (for Rattus, $P<0.001$; Spermophilus, $P<0.01$; Mustela, $P<0.001$; Oryctolagus, $P<0.05$; Didelphis, $P<0.05$). Anaesthesia did not significantly affect normal water loss in any species ($P>0.05$ for all species).

Nasal temperatures were below normal core body temperature in all species (Table 3), ranging from 2.6°C above ambient temperature in Rattus, to 6.6°C above ambient in Spermophilus.

In the control treatments, the estimated cutaneous components amounted to 27% of EWL in Rattus, Mustela and Oryctolagus, 29% in Spermophilus, and 45% in Didelphis.

The estimated respiratory (RWL) portions of EWL for control and experimental treatments are compared in Fig. 3. Respiratory water loss in the experimental, orally breathing animals was increased by about 36% - 143% over that of control animals, using nasopharyngeal breathing.

Discussion

In all five species, nasal temperatures of normal animals were considerably less than body temperature (Table 3), and nasopharyngeal breathing resulted in substantially lower respiratory water loss than when the nasal passages were occluded (Fig. 3). These data strongly suggest the presence of a mechanism reducing respiratory water loss in the nasal passages of these animals, and that this mechanism involves countercurrent exchange of heat and water at the turbinates, as described in the Introduction.

The taxa in this study represent one marsupial and three placental orders. None of these species usually inhabit deserts or other xeric environments. Other studies have revealed that cooling of expired air to below core body temperature can be observed in at least nine mammalian orders, encompassing a range of environments (Table 1). As Schmid (1976) suggested, this phenomenon is probably indeed universal among mammals. There is generally very little difference in the extent of cooling of expired air between desert and non-desert animals (Schmidt-Nielsen et al. 1970b), or between mammals from different phylogenetic groups (Schmid 1976; Hill 1978; Table 3).

These observations, combined with the almost ubiquitous presence of complex turbinates among mammals, imply that this mechanism for respiratory water recovery probably did not evolve as an adaptation to any particular modern

environment. Instead, it appears that recovery of heat and water from exhalant air is of intrinsic importance to all members of this class.

Loss of respiratory heat and water is a potentially serious problem for all mammals as a result of their high ventilation rates: respiratory water loss accounts for up to 73% of total evaporative water loss among the mammals in this study, even with turbinal recovery of respiratory water, and under resting conditions at a relatively low ambient temperature. In contrast, respiratory water loss represents only 13% - 56% of total evaporative water loss in reptiles (Tracy 1982), which have metabolic rates only about one-third to one-tenth of mammalian rates (Dawson and Hulbert 1970; Bennett and Dawson 1976). Control of respiratory water loss, aside from osmoregulatory considerations (eg. Jackson and Schmidt-Nielsen 1964; Schmidt-Nielsen et al. 1981), also has a significant effect on mammalian heat budgets. In cold environments, cooling of exhaled air can substantially reduce respiratory heat loss (Blix and Johnsen 1983; Langman 1985; Folkow and Blix 1987), while under conditions of heat stress, cooling of expired air may be abandoned during panting, to regulate body temperature (eg. Schmidt-Nielsen et al. 1970a) or even brain temperature independently (eg. Taylor and Lyman 1972; Baker 1982; Johnsen et al. 1987; Schroter et al. 1989).

Heat exchange in the upper respiratory passages is not unique to mammals. It is, for example, also known in

thermoregulating reptiles, which lack complex turbinates (Murrish and Schmidt-Nielsen 1970). In fact, it probably occurs to some extent in all thermoregulating air-breathers (Schmidt-Nielsen 1984; Schroter and Watkins 1989). However, the high ventilation rates of mammals necessitate narrow nasal passage ways for complete exchange of heat and water (Schroter and Watkins 1989). These authors found that the gap width between adjoining turbinal lamellae in several medium to large mammals (both desert and non-desert, and from various phylogenetic groups) is narrow enough to allow complete heat exchange during resting respiration rates, and in most species during exercise as well. Furthermore, gap widths can be altered by erectile linings of the turbinates, while the amount of air flowing through the turbinate complex can be regulated in many species by a swell body, located below the turbinates (Negus 1958; Schroter and Watkins 1989).

To illustrate the efficiency of this system, resting oxygen consumption rates and estimated respiratory water loss for two species of mammals and two similar-sized, thermoregulating reptiles are compared (Fig. 4). As a result of their higher metabolic rates, the mammals lose more water per minute than the reptiles. But while the mammalian oxygen consumption is 11x - 17x greater than the reptilian rates, their respiratory water loss is only two to five times greater than the reptilian rate (Fig. 4a). Furthermore, increased oxygen consumption also results in

increased metabolic water production. At an average of 0.54 mg H_2O/ml O_2 (Schmidt-Nielsen 1964: p. 30), metabolic water production of the mammals equals or even slightly exceeds respiratory water loss at this ambient temperature (cf. MacMillen and Hinds 1983), whereas metabolic water production contributes relatively little to alleviate respiratory water loss in the reptiles (Fig. 4b). These data suggest that complex nasal turbinates can significantly reduce, if not eliminate, the magnitude of respiratory water loss associated with high, mammalian metabolic rates.

The values in this example are for resting conditions. During exercise, metabolic demands, and thus ventilation rates, are higher, and respiratory water loss is likely to be greater. However, for a similar proportionate increment, respiratory water loss would in absolute terms be much greater for mammals than for reptiles. The effects of turbinates on RWL during activity have not been studied extensively, but Schroter and Watkins (1989) suggest that nasal heat and water exchange may be fully functional during moderate exercise in mammals. If so, the water-conserving effect of mammalian turbinates may be even more significant during periods of activity.

Significantly, a fairly well-developed turbinate system is present in several orders of birds, all of which have metabolic rates at least as high as those of mammals (Bang 1961, 1964, 1966, 1968; Schmidt-Nielsen et al. 1970b). Avian turbinals are usually loosely scrolled (Fig. 2) and,

as in mammals, are functionally separated into respiratory and olfactory types. Cooling of expired air and the resultant reduction of respiratory water loss also occur in birds (Schmidt-Nielsen et al. 1970b; Berger et al. 1971; Murrish 1973), even though the turbinal complex of birds is generally not as elaborate as that of mammals. The avian respiratory system is more efficient than the mammalian system, however, and capable of greater oxygen extraction (Bernstein and Schmidt-Nielsen 1974; Piiper 1989). Consequently, birds have relatively lower ventilation rates than mammals (Lasiewski and Calder 1971; Schmidt-Nielsen 1984, 1990) so that the simpler turbinal configuration may be adequate for respiratory heat exchange and water recovery.

In summary, several lines of evidence strongly suggest that reduction of respiratory water loss by turbinate cooling of expired air is an intrinsic feature of many, if not all, mammals. Because of their high ventilation rates, respiratory water loss is of much greater potential importance in mammals than in reptiles, and the need for its reduction is more immediate. Complex turbinates allow effective heat/water transfer between expired air and nasal mucosa even at high mammalian ventilation rates. These data suggest that the complex maxilloturbinates of mammals probably evolved to compensate for the high respiratory water loss associated with high ventilation rates, rather than for specific environmental conditions <u>per se</u>. It is

possible that the scrolled respiratory turbinals in birds represent an analogous adaptation. It should be emphasized that in both birds and mammals, olfactory sensory tissues are located on a different set of turbinals, in a spacially distinct region.

Evolutionary Implications

Bennett and Ruben (1979) suggest the development of increased aerobic capacity, to support greater sustainable activity, was a principal factor in the evolution of mammalian endothermy. Concomitantly, both resting and active ventilation rates gradually increased, perhaps five- to tenfold over ancestral rates. In this case, turbinates may have evolved to counteract the increase in respiratory water loss that would necessarily have accompanied the evolution of mammalian endothermy.

All living monotremes, marsupials and eutherian mammals are fully endothermic. All have metabolic levels which are essentially similar when adjusted to a common body temperature, and are substantially greater than reptilian levels (Dawson and Hulbert 1970; Bennett and Dawson 1976; Hulbert 1980; cf. Jenkins 1990). Moreover, key features of oxygen procurement and delivery systems, such as alveolar lungs, four-chambered heart, non-nucleated red blood cells, hematocrit levels and blood oxygen carrying capacity are

also similar, if not identical, in these groups (Bennett and Ruben 1986).

Although the phylogenetic position of monotremes is subject to debate, the primitive nature of the postcranial skeleton of monotremes suggests that this group diverged from the other mammals at a relatively early stage, probably fairly soon after the origin of mammals (Carroll 1988; Szalay 1990). Therefore, these features of metabolic physiology were probably present early in mammalian history, and it is generally agreed that endothermy probably had already been attained when mammals arose in the late Triassic (Bennett and Ruben 1986; Carroll 1988).

Pelycosaurs, primitive synapsid reptiles of the Late Carboniferous-Permian, are usually considered to have been ectotherms with typical reptilian respiration rates, and capable of behavioral thermoregulation (Kemp 1982; Turner and Tracy 1986). Consequently, expansion of aerobic metabolic capacities, which ultimately led to the evolution of endothermy, probably took place among therapsids, the Permo-Triassic mammal-like reptiles intermediate between pelycosaurs and mammals. While the specific thermoregulatory status of the various groups of therapsids remains uncertain (cf. Bennett and Ruben 1986), progressive changes in their post-cranial skeleton certainly suggest increasingly mammal-like activity levels (Jenkins 1970; Kemp 1982; Colbert 1986).

The Late Permian and Triassic Periods were marked by a general warming of global climates (Parrish et al. 1986). Tropical and subtropical belts appear to have been relatively wide, and expanding. Continental glaciation, which had occupied much of southern Pangaea during the Carboniferous and Early Permian, had all but disappeared by the end of the Permian (Caputo and Crowell 1985; Parrish et al. 1986). In fact, in the Triassic, the high latitudes had become inhabited by various kinds of reptiles and amphibians, which indicates that even in these regions temperate conditions may have prevailed (Parrish et al. 1986), although recent computer simulations suggest that pangaeic winters at high latitudes may still have been rather cold (Crowley et al. 1989; Kutzbach and Gallimore 1989). The Triassic was also a period of severe aridity. Widespread evaporite deposits of this age (Fig. 6) indicate that much of Pangaea, particularly its interior, was very dry, either year-round or seasonally (Robinson 1973; Parrish et al. 1986; Boucot in prep.; see also Kutzbach and Gallimore 1989).

Under such globally warm conditions, ectotherms would probably have had little problem with thermoregulation through behavioral or inertial means. Although they may have had to hibernate in cold winters at high latitudes, therapsids, like modern reptiles (see, eg. Huey and Slatkin 1976; Huey 1982), probably could have easily maintained relatively high and constant body temperatures even before

endothermy had evolved, at least when they were active (cf. Turner and Tracy 1986). It is, therefore, reasonable to assume that some temperature gradient existed in their respiratory passages.

However, expansion of the aerobic capacities of therapsids during this period was very likely accompanied by increases in their ventilation rates, and therefore by increased rates of respiratory water loss. Furthermore, increased stamina and activity would have allowed prolonged periods of elevated metabolism, with further increases in respiratory water loss. In addition, many therapsids, particularly many of the more advanced forms later in the Triassic, were comparatively small (cf. Kemp 1982), and the first mammals were as small as modern shrews and mice (Crompton and Jenkins 1979). Small animals have relatively greater ventilation rates than large ones (Schmidt-Nielsen 1970, 1984), and, consequently, relatively high respiratory water losses. Small animals also have a relatively large surface area, over which cutaneous evaporation takes place, but a relatively small volume for storage of water. Consequently, the small size of these animals would have aggravated their water-related problems, especially those brought on by increases in respiration rate.

Under these circumstances, it seems very likely that, sooner or later, mechanisms for water conservation would have evolved, particularly considering the arid conditions of this period. Narrowing the effective gap width of the

nasal passages with turbinates would have allowed therapsids to control the nasal temperature gradient already present, enabling them to cool expired air and thus to reduce respiratory water loss at little or no energetic cost. Even reduction of expired air temperature by only five degrees would have reduced effective respiratory water loss (RWL minus metabolic water produced) by about 50%. Successive increases in ventilation rate and respiratory water loss could have been compensated simply by concurrent increases in the size and complexity of the turbinates. Since turbinates aid in reducing respiratory water loss in virtually all living descendants of therapsids, it is highly probable that this was the original impetus for their evolution.

Unfortunately, there is little direct fossil evidence of turbinates among therapsids. These thin and fragile bones are seldom if ever preserved in fossils, even among recent mammals. Furthermore, the turbinates may well have been cartilaginous in the early stages of their evolution, as are the conchae of living reptiles (Parsons 1967). However, mammalian turbinals attach to longitudinal ridges on the internal surface of the nasal cavity. Such ridges are present, among others, in multituberculates (eg. Miao 1988) and in Morganucodon, the oldest known mammal (Kermack et al. 1981). Similar ridges have been described for several therapsids as well (eg. Watson 1913, 1931; Brink 1956; Hopson 1969; Fourie 1974; Kemp 1969, 1979, 1980, 1982).

Furthermore, there may be other aspects of the rostral morphology that might provide indirect information about the possible existence of turbinates in these animals. For example, the secondary palate is generally interpreted as a separation between air and food passages, to ensure continuous breathing during mastication (Brink 1956; Romer and Parsons 1986; Carroll 1988), or as a structural reinforcement of the upper jaw (Thomason and Russell 1986). However, without a secondary palate floor to the nasal passage to channel air across the maxilloturbinates, these structures probably would have little effect on respiratory water loss. Significantly, a secondary palate was best developed among advanced therapsids, the taxa most likely to have had elevated pulmonary ventilation rates (Moore 1981; Kemp 1982; Romer and Parsons 1986). Finally, the volume of the nasal cavity, particularly of the respiratory portion, in front of the transverse lamina (primary palate), may possibly provide clues on whether there was sufficient space to accommodate a maxilloturbinate complex.

In conclusion, there is substantial evidence indicating that complex mammalian turbinates probably evolved to reduce respiratory water loss associated with high ventilation rates. The evidence suggests that they are of great antiquity, and may have originated among therapsids, in concert with the development of increased aerobic capacity, sustainable activity and, ultimately, endothermy. Ridges in the nasal cavities of advanced therapsids, possibly

representing attachment sites of turbinates, provide some tentative support for this idea. A reexamination of the nasal cavity of therapsids may reveal whether more conclusive evidence of respiratory turbinals can be found. Presence of maxilloturbinals would be a strong indication of expanded ventilation rates and aerobic capacities in these animals.

Acknowledgements

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Table 1: Mammalian orders and families in which reduced expired air temperatures have been recorded (the number of species studied in each family in parentheses)

I DESERT ANIMALS

order	family	sources
Rodentia		
	Heteromyidae (2)	Jackson and Schmidt-Nielsen 1964; Schmidt-Nielsen et al. 1970b; Collins et al. 1971
	Muridae (1)	Withers et al. 1979b
Artiodactyla		
	Giraffidae (1)	Langman et al. 1979
	Bovidae (6)	Langman et al. 1979; Kamau et al. 1984
	Camelidae (1)	Schmidt-Nielsen et al. 1981b
Perissodactyla		
	Equidae (1)	Langman et al. 1979

II NON-DESERT ANIMALS

Marsupialia		
	Didelphidae (1)	Hill 1978; present study
Insectivora		
	Soricidae (2)	Schmid 1976

Chiroptera		
	Vespertilionidae (3)	Schmid 1976
Rodentia		
	Muridae (10)	Jackson and Schmidt-Nielsen 1964; Getz 1968; Schmid 1976; Bintz and Roesbery 1978; Withers et al. 1979a; Edwards and Haines 1978; present study
	Sciuridae (10)	Schmid 1976; Bintz and Roesbery 1978; Withers et al. 1979a; Welch 1984; present study
Lagomorpha		
	Leporidae (2)	Schmid 1976; Caputa 1979; present study
Carnivora		
	Mustelidae (3)	Schmid 1976; Withers et al. 1979a; present study
	Canidae (2)	Verzar et al. 1953; Schmid 1976
	Phocidae (1)	Folkow and Blix 1987
	Otariidae (1)	Huntley et al. 1984
Artiodactyla		
	Cervidae (1)	Blix and Johnsen 1983; Langman 1985
Primates		
	Hominidae (1)	Cole 1953; Proctor et al. 1977

Table 2: Evaporative water loss (EWL) and oxygen consumption ($\dot{V}O_2$) in 5 species of small mammals, comparing intact control (C), anaesthetized (A) and experimental animals with plugged nares(E). T_a = 15.0 ± 2.0°C

species	treat-ment	n*	EWL (mg H_2O/ml O_2)	$\dot{V}O_2$ (ml O_2/min)
Rattus	C	11	0.64 ± 0.02	7.83 ± 0.37
(mean Mass: 283 g)	A	5	0.62 ± 0.01	6.39 ± 0.28
(F= 1.14 l/min)*	E	6	0.81 ± 0.02	7.46 ± 0.51
Spermophilus	C	10	0.75 ± 0.04	11.82 ± 0.61
(mean Mass: 596 g)	A	4	0.69 ± 0.03	11.97 ± 1.46
(F= 1.61 l/min)	E	6	1.04 ± 0.10	13.59 ± 1.48
Mustela	C	7	0.70 ± 0.02	19.38 ± 0.75
(mean Mass: 830 g)	A	4	0.78 ± 0.03	17.09 ± 0.61
(F= 3.22 l/min)	E	4	0.93 ± 0.03	18.62 ± 0.86
Oryctolagus	C	5	0.89 ± 0.03	36.55 ± 4.71
(est. Mass: 3.0 kg)	A	4	0.85 ± 0.02	33.95 ± 3.49
(F= 5.57 l/min)	E	4	1.17 ± 0.13	26.68 ± 2.64
Didelphis	C	4	0.91 ± 0.03	32.74 ± 5.42
(est. Mass: 3.3 kg)	A	4	0.97 ± 0.07	31.21 ± 3.53
(F= 5.57 l/min)	E	4	1.58 ± 0.18	37.21 ± 2.60

* F = Flow rate, n = number of individuals

Table 3: Nasal temperatures of 5 species of small mammals

species	n	$T_{ambient}$ (°C)	T_{nasal} (°C)	ΔT[1] (°C)	T_{body}[2] (°C)
Rattus	9	15.4 ± .27	17.9 ± .18	2.6 ± .21	37.0 ± 1
Spermophilus	5	15.4 ± .51	19.7 ± .69	4.4 ± .54	37.0 ± 1
Mustela	5	14.3 ± .16	17.8 ± .49	3.5 ± .35	37.0 ± 1
Oryctolagus	8	15.3 ± .52	21.9 ± .66	6.6 ± .52	37.0 ± 1
Didelphis	5	15.5 ± .11	17.9 ± .37	2.4 ± .32	35.5 ± .5

1 $\Delta T = T_{nasal} - T_{ambient}$.

2 Schmidt-Nielsen 1990.

Figure 1. Raccoon (Procyon lotor) skull, right sagittal section. For abbreviations, see p. 135.

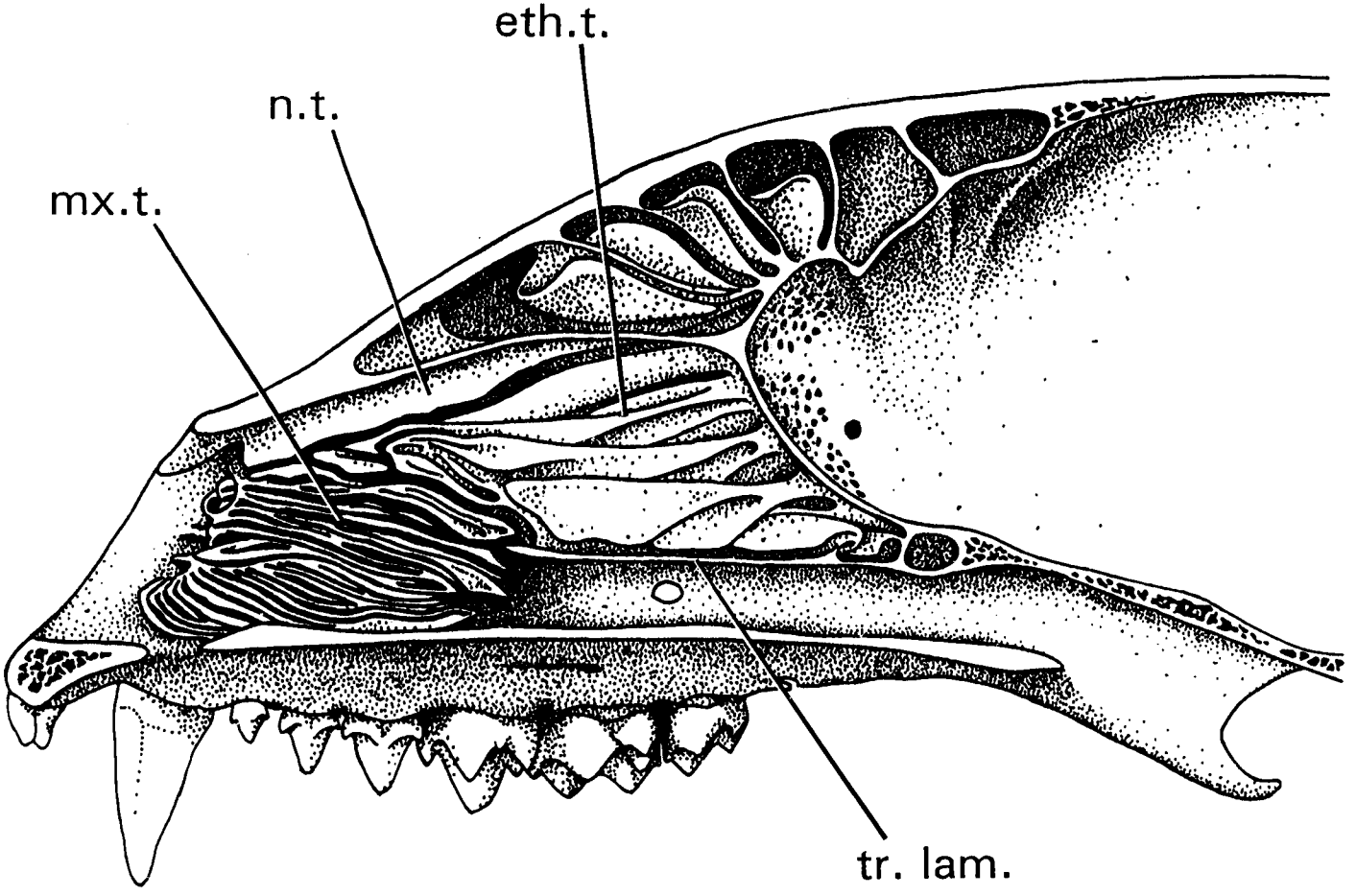
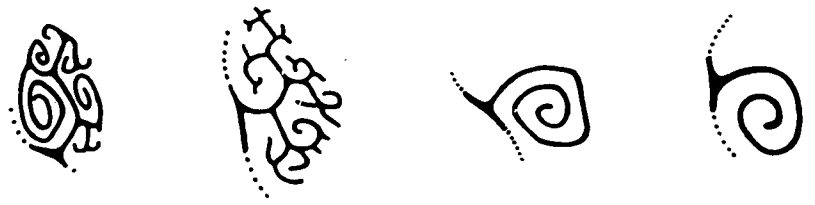

eth.t.
n.t.
mx.t.
tr. lam.

Figure 2. Cross-sections of maxilloturbinals of several mammalian species, and of the respiratory turbinals of two species of birds (not to scale). Homo, Bison, Dendrolagus and Phoca after Negus 1958; Meles after Anthony and Iliesco 1926; Caenolestes after Broom 1926; Fulmarus after Bang 1966; Coragyps after Bang 1964.

Homo Bison Meles Phoca



Dendrolagus Caenolestes Fulmarus Coragyps

Figure 3. Estimated rates of respiratory water loss (RWL) of five mammalian species. Data are obtained from resting animals, under control and experimental conditions (see text). T_a = 15°C. No error bars are given; see Table 1 for standard errors of original data.

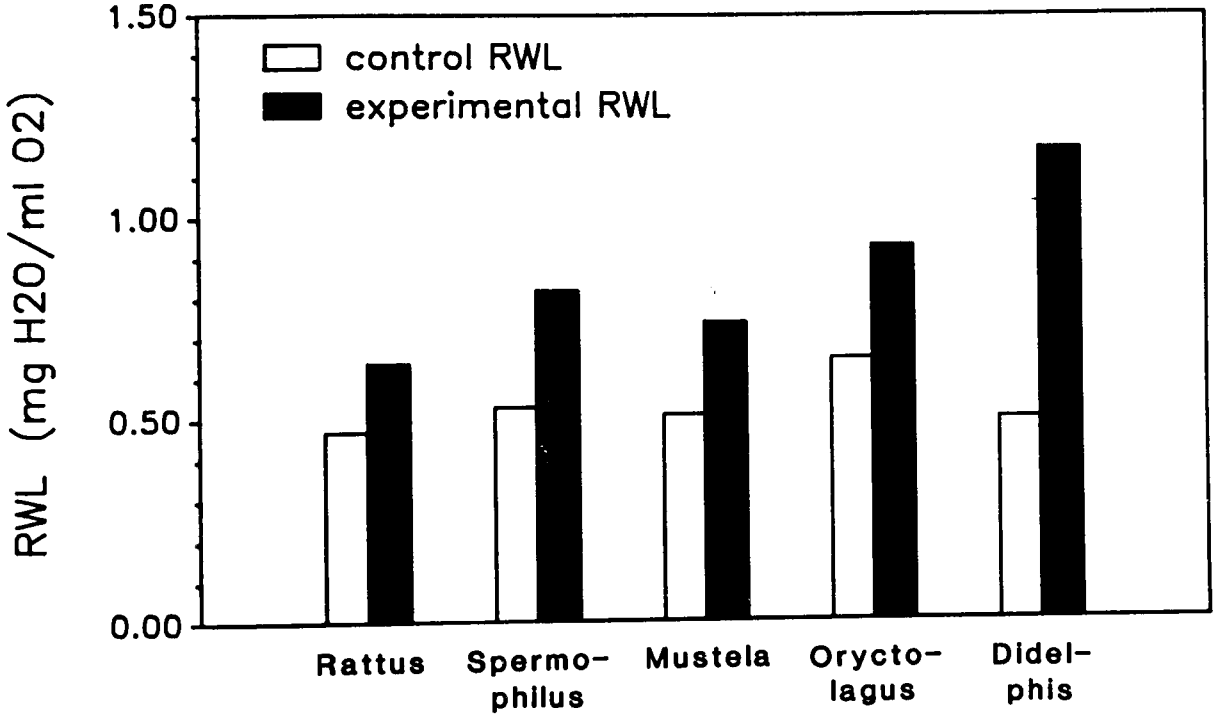
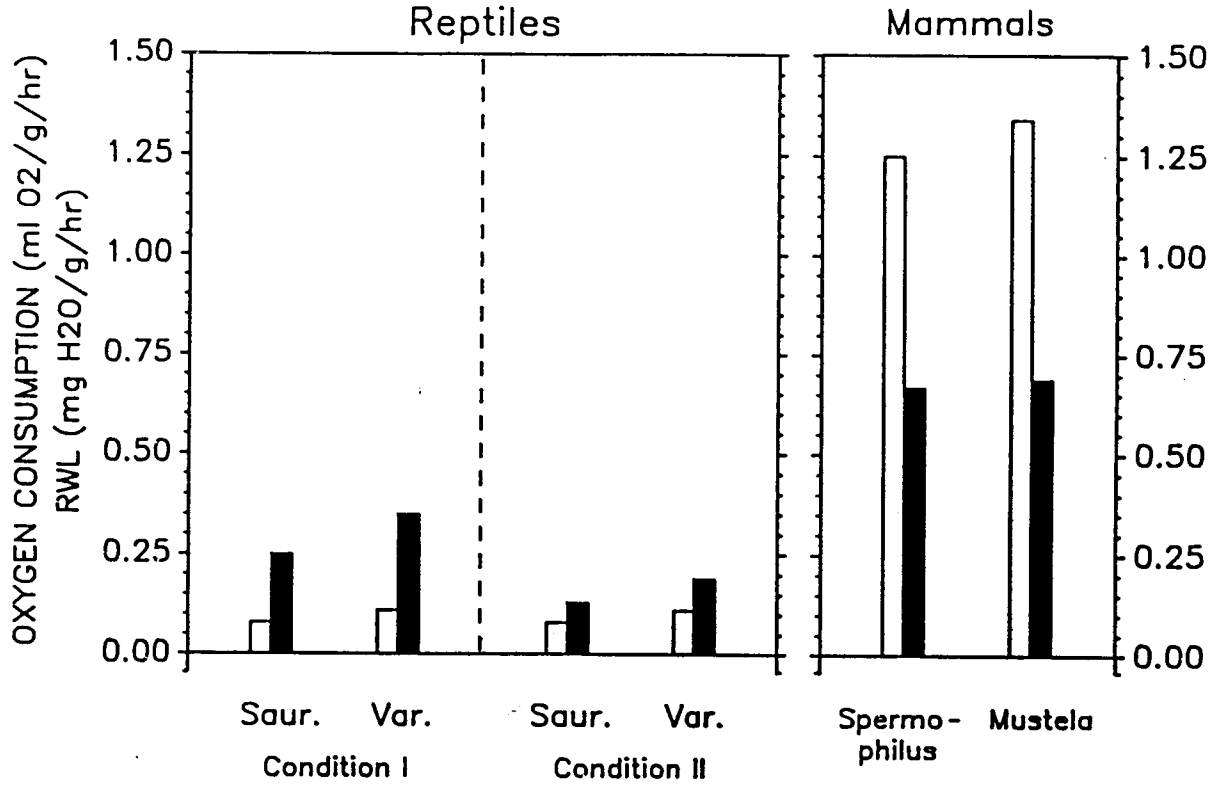

1.50
1.00
0.50
0.00
RWL (mg H2O/ml O2)
control RWL
experimental RWL
Rattus
Spermo-
philus
Mustela
Orycto-
lagus
Didel-
phis

Figure 4. Comparison of reptilian and mammalian oxygen consumption and respiratory water loss rates. A. Comparison of resting oxygen consumption (open bars) and respiratory water loss (filled bars) for two mammals (Spermophilus, 596 g, and Mustela, 830 g) and two thermoregulating reptiles (Sauromalus, 574 g, and Varanus, 674 g), breathing dry air at T_a = 15°C. B. Similar, but with respiratory water loss reduced by metabolic water production.

Mammalian data from Table 1 and Figure 3. Reptilian oxygen consumption after Bennett 1972, 1973, for T_b= 37°C. Respiratory water loss for reptiles was estimated assuming no cooling of exhaled air (condition I), or cooling of exhaled air to 25°C (condition II; extrapolated from Murrish and Schmidt-Nielsen 1970).


Reptiles
Mammals
OXYGEN CONSUMPTION (ml 02/g/hr)
RWL (mg H2O/g/hr)
1.50
1.25
1.00
0.75
0.50
0.25
0.00
Saur.
Var.
Saur.
Var.
Condition I
Condition II
Spermo-
philus
Mustela

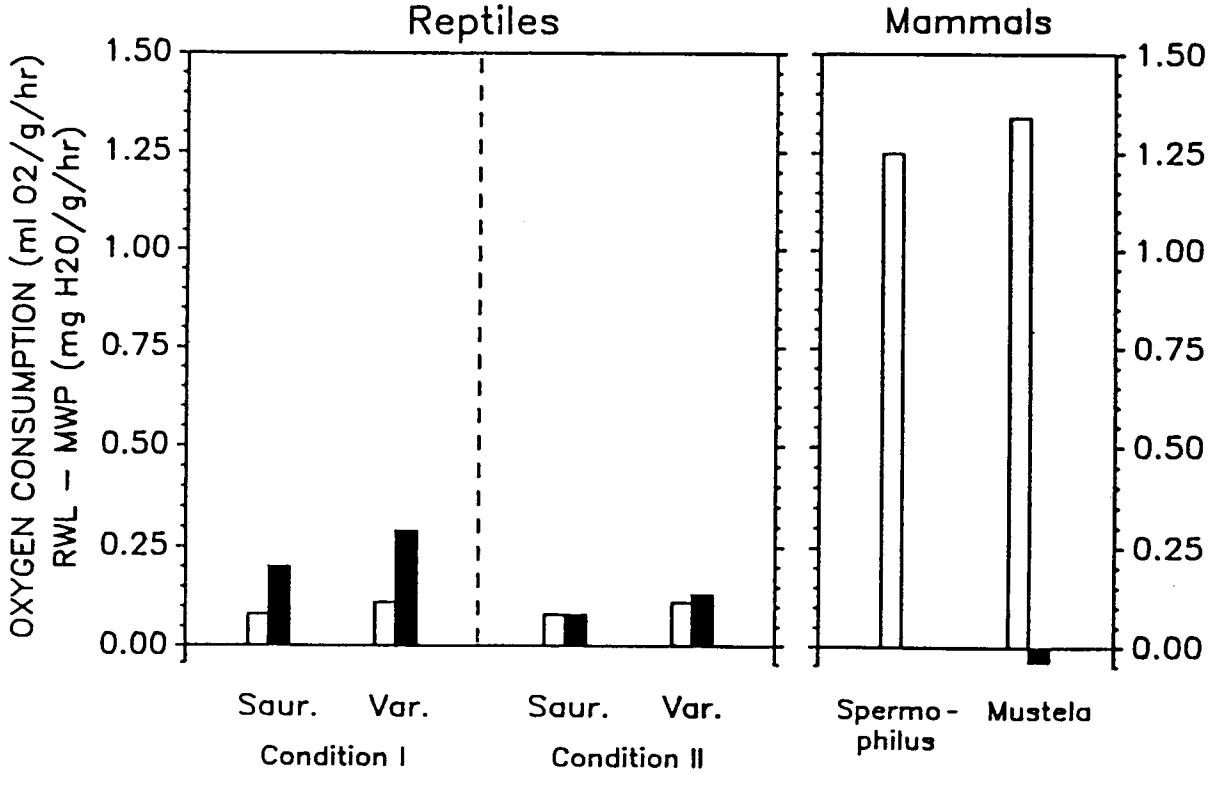
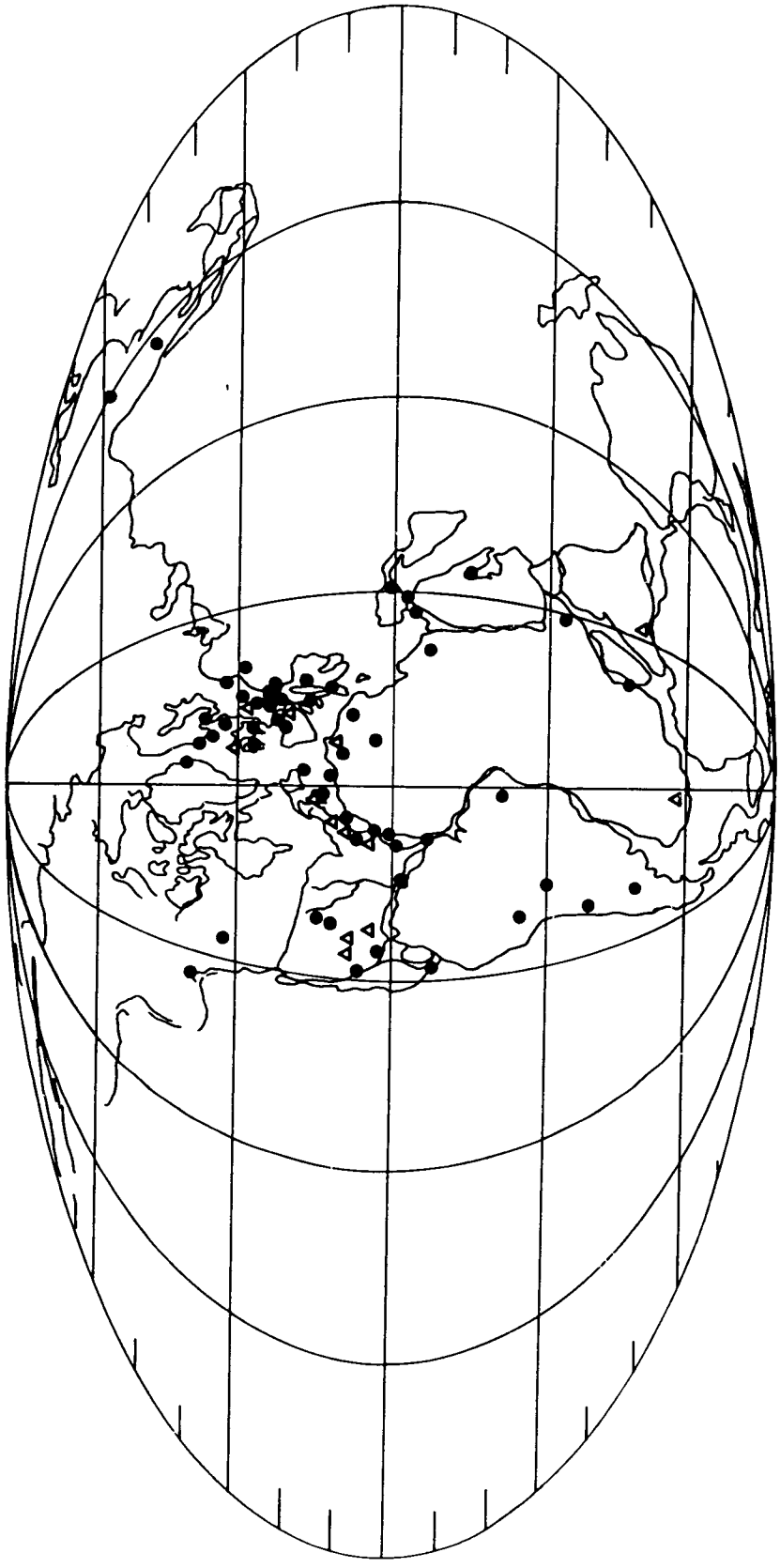

Reptiles
Mammals
OXYGEN CONSUMPTION (ml 02/g/hr)
RWL – MWP (mg H2O/g/hr)
1.50
1.25
1.00
0.75
0.50
0.25
0.00
Saur.
Var.
Saur.
Var.
Condition I
Condition II
Spermo-
philus
Mustela

Figure 5. Evaporite and calcrete deposits of Triassic age. Evaporites (circles) are indicative of year-round or seasonal aridity; calcretes (triangles) are formed in semi-arid, warm to cool-temperate environments. Data from Boucot (in prep.). Base map is a Pangaeic reconstruction for the Mid-Triassic, after Condie 1982.



CHAPTER 3

TURBINATES IN THERAPSIDS: EVIDENCE FOR LATE PERMIAN ORIGINS OF MAMMALIAN ENDOTHERMY

by

Willem J. Hillenius

This manuscript has been invited for submission to

EVOLUTION

Abstract

The structure and function of the nasal conchae of reptiles, birds and mammals are reviewed, and the relationships to endothermy of the mammalian elements are examined. Reptilian conchae are relatively simple, recurved structures, which bear primarily olfactory epithelium. Conversely, the conchae, or turbinals, of birds and mammals are considerably more extensive and complex, and bear, in addition, respiratory epithelium. Of the mammalian turbinates, only the exclusively respiratory maxilloturbinal has a clear functional relationship with endothermy, as it reduces desiccation associated with rapid and continuous pulmonary ventilation (Hillenius 1992). The other mammalian turbinates principally retain the primitive, olfactory function of the nasal conchae.

In fossil mammals and mammal-like reptiles, the presence and function of turbinates is most readily revealed by the ridges by which they attach to the walls of the nasal cavity. Ridges for olfactory turbinals are located posterodorsally, away from the main current of respiratory air-flow, whereas those of the respiratory turbinals are situated in the anterolateral portion, directly in the path of respired air. The maxilloturbinal is also characterized by its proximity to the ostium of the nasolacrimal duct.

These studies of the nasal cavities of fossil synapsid reptiles indicate that, while olfactory turbinals may be

found among the earliest members of this lineage, respiratory turbinals first appeared in primitive therocephalians and cynodont therapsids. This suggests that the evolution of "mammalian" oxygen consumption rates may have begun as early as the Late Permian, and developed in parallel in therocephalians and cynodonts. Full mammalian endothermy may have taken as much as 40 to 50 million years to develop.

Introduction

Endothermy, or "warm-bloodedness," is among the most significant features that distinguish living mammals and birds from reptiles and other vertebrates. Endothermy allows mammals and birds to maintain a high and relatively constant body temperature, even at rest, in the face of a wide range of ambient conditions (Schmidt-Nielsen 1990). Moreover, the increased aerobic capacity associated with endothermy enables these animals to sustain levels of activity well beyond the scope of ectotherms (Bennett and Ruben 1979; Bennett 1982, 1991). These factors, stamina and thermal independence, very likely contribute to a large degree to the present success of mammals and birds (Willson 1984; Bennett and Ruben 1986), and it is therefore not surprising that the evolution of endothermy has received considerable attention (e.g., Hopson 1973; McNab 1978, 1983; Crompton et al. 1978; Bennett and Ruben 1979; Dawson and Grant 1980; Hulbert 1980, 1987; Taylor 1980; Else and Hulbert 1981, 1985; Bennett 1991; Ruben 1991).

Unfortunately, despite its profound significance, endothermy has been difficult to demonstrate in extinct forms (see Thomas and Olson 1980; Bennett and Ruben 1986; McGowan 1991). Key attributes of endothermy, such as complex lungs, elevated blood oxygen carrying capacity, mitochondrial density, etc. (Bennett and Ruben 1979, 1986; Else and Hulbert 1981, 1985), are not preserved in fossils.

Conversely, many of the features often used to infer the presence of endothermy in extinct vertebrates, such as bone histology, posture and predator-prey ratios, have proven unreliable (Bennett and Dalzell 1973; Bennett and Ruben 1986; Reid 1987; King 1990). In the mammalian lineage, Bennett and Ruben (1986) considered only one anatomical trait to be very suggestive of endothermy: the presence of nasal turbinate structures in certain therapsid reptiles.

In a previous paper (Hillenius 1992), I presented experimental evidence that supports a strong association between endothermy and the respiratory turbinates of mammals, the maxilloturbinal bones. These structures are likely to have evolved in concert with the development of enhanced aerobic capacity and activity levels among the reptilian ancestors of mammals, the mammal-like reptiles or therapsids (Hillenius 1992). However, the turbinates most frequently cited with reference to endothermy in therapsids have been ethmoturbinals (e.g. Watson 1913; Brink 1956; Van Valen 1960; Bennett and Ruben 1986). In extant mammals, the ethmoturbinals function primarily in olfaction, and these structures have no particular correlation with endothermy. Heretofore, no evidence for the existence of strictly respiratory turbinals has been described for mammal-like reptiles, although they are known in early mammals (e.g. Kermack et al. 1981; Miao 1988; Lillegraven and Krusat 1991).

In the present paper, I review the relationships between mammalian nasal turbinates and endothermy, as well as the presence of turbinates in the fossil record of early mammals and therapsids. Newly prepared fossil material suggests that respiratory turbinals did occur among therocephalians and cynodonts, two groups of advanced therapsids. This suggests that these animals probably possessed expanded ventilation rates, and that the evolution of endothermy may have begun in the Late Permian, some 40 to 50 million years prior to the appearance of the first mammals.

Turbinate form and function

In most amniote tetrapods, the lateral walls of the nasal cavity exhibit one or more conchal projections, which provide additional surface area for nasal epithelia (Matthes 1934; Parsons 1971; Romer and Parsons 1986). However, there are two significant differences between the conchae of reptiles and those of birds and mammals. Whereas reptilian conchae have a relatively simple shape (Fig. 6), in birds and mammals these structures are considerably more extensive and complex (Figs. 7-10), and are often called turbinates (Lat. turbo, whirlwind) to reflect this increased complexity. Furthermore, reptilian conchae are covered only with sensory (olfactory) tissue, whereas the turbinates of birds and mammals, in addition, bear extensive respiratory (i.e., pseudostratified mucociliated) epithelium.

Among living reptiles, the conchae typically consist of a simple, partially coiled, cartilaginous process (Fig. 6) that is almost exclusively olfactory in function. In lizards and snakes there is generally a single concha, located dorsally in the olfactory region of the nasal cavity (Fig. 6a), and covered primarily with sensory epithelium (Matthes 1934; Parsons 1970, 1971). In some forms, the concha may enclose a salt gland, the lateral nasal gland (Fig. 6c; Parsons 1970). In Sphenodon, two conchae are present (Parsons 1970, 1971), likewise in the olfactory portion of the nasal cavity. Crocodilians have a somewhat

more complex nasal cavity, with three conchae located in succession in the elongate nasal passage, alternating with a series of sinuses and recesses (Fig. 6b). Nevertheless, their conchae retain the simple, recurved shape typical of other reptiles (Fig. 6c). All three conchae of crocodiles remain in the nasal olfactory region, dorsal and posterior to the main respiratory air passage, and are primarily covered with sensory epithelium. However, some respiratory epithelium occurs on the ventral portion of the anterior concha, which is exposed to the respiratory airstream (Matthes 1934, Parsons 1970, 1971). Conchae are absent in turtles (Parsons 1970, 1971; Romer and Parsons 1986).

The turbinates of endotherms, on the other hand, are considerably more extensive and complex. Furthermore, olfactory epithelium is restricted to the posterior turbinates only; the more anterior turbinates are covered strictly with respiratory epithelium.

In birds, the extent and complexity of the nasal cavity varies widely with the shape of the bill, but in general, the avian nasal passage is elongate with three cartilaginous turbinates in succession (Fig. 7). The anterior turbinal is usually relatively simple, but the others, especially the middle turbinal, are often more highly developed into prominent scrolls with multiple turns (Fig. 7b; Matthes 1934; Portmann 1961; Bang 1971; Parsons 1971). Sensory (olfactory) epithelium is restricted to the posterior turbinal, which is positioned outside the main air

stream (Fig. 7a), sometimes in a separate olfactory chamber (e.g., Bang 1966). The posterior turbinal is most extensive in taxa with a well developed olfactory sense, such as some cathartid vultures (Bang 1964), tube-nosed birds (Wood-Jones 1937a, b; Bang 1966; Wenzel 1986), and kiwis (Matthes 1934; Portmann 1961). Conversely, it is much reduced in other forms, such as pigeons (Matthes 1934; Bang 1971; Parsons 1971).

The anterior and middle turbinals of birds are situated in the respiratory passage (Fig. 7a), and are covered primarily with mucociliated respiratory epithelium (Bang and Bang 1959; Parsons 1971). The middle turbinal is usually the largest and most elaborate in the avian nasal cavity (Fig. 7b; Matthes 1934; Portmann 1961; Bang 1964, 1966, 1971). These structures are well situated to modify bulk respired air, and probably have a function similar to the mammalian maxilloturbinals, discussed below.

In mammals, the turbinates are highly developed, and exceed those of other tetrapods in size, number and complexity (Figs. 8-10). Mammalian turbinates are also largely ossified. Three types are recognized. Posteriorly, a large number of ethmoturbinals typically fill the olfactory portion of the nasal cavity (Fig. 8). These are convolutely scrolled and densely packed structures, which make up the "ethmoidal labyrinth." Some authors further subdivide the ethmoturbinals into ecto- and endoturbinals, where the latter project farther medially, and are visible

in a mid-sagittal section (Allen 1882; Paulli 1900a, b, c; Matthes 1934; Moore 1981). The ethmoturbinals are primarily covered with sensory epithelium (Matthes 1934; Negus 1958; Bang and Bang 1959; Moore 1981).

A single nasoturbinal extends from this region anteriorly along the roof of the nasal cavity (Fig. 8). It is often considered one of the ethmoturbinals (e.g., Allen 1882; Paulli 1900a, b, c; Allison 1953; Moore 1981), as at least part of it appears to have the same embryonic origin as the latter. The nasoturbinate usually consists of a simple, elongate lamella, but may be branched in small rodents (Fig. 9); it bears sensory epithelium posteriorly, but the anterior portion is often covered with respiratory tissue.

The maxilloturbinal is the most extensive and complex mammalian turbinal element. It occupies the anteroventral portion of the nasal cavity (Fig. 8), and is covered exclusively with ciliated respiratory epithelium. Its morphology is highly diverse (Fig. 9), and is correlated primarily with phylogenetic affinity (Matthes 1934; Negus 1958; Moore 1981; Hillenius 1992). For example, in artiodactyls, the maxilloturbinates typically consist of large, double scrolls, whereas most carnivores have finely branched structures (Fig. 9). In a few groups, such as cetaceans and higher primates, the turbinates are reduced in size (Fig. 9). The maxilloturbinal has no sensory function, and is positioned so that air must pass over it

during inspiration and expiration (Figs. 8, 10). It serves an important function in warming and humidifying inhaled air, and filtering out particulate matter (Negus 1956, 1958; Walker et al. 1961). Perhaps the most significant functional aspect of the maxilloturbinal, however, is its ability to reduce respiratory water loss, by cooling and dehumidifying exhaled air (Jackson and Schmidt-Nielsen 1964; Collins et al. 1971). This phenomenon occurs not only in desert mammals, where it was first described, but is probably an intrinsic feature of all mammals (Hillenius 1992).

The ethmoturbinals, alternately, are incapable of modifying large volumes of air. Their configuration in the posterior portion of the nasal cavity inhibits air movement: they are situated outside the path of respiratory air, generally at an angle to the airstream (Fig. 8), and their structure partitions the olfactory space into a series of blind recesses. A transverse lamina often further isolates them from the airstream. Consequently, the space occupied by the ethmoturbinals is ordinarily not ventilated, except during deliberate "sniffing" (Fig. 10; Lucas and Douglas 1934; Dawes 1952; Becker and King 1957; Evans and Christensen 1979). Apparently, effective olfactory analysis requires low air-flow velocity, and airborne odorants may ordinarily reach the sensory epithelium only by diffusion (Moore 1981). In carnivores, which have an especially well-developed sense of smell, ethmoturbinals may even invade the

frontal and sphenoid sinuses, which are never ventilated (Negus 1958; Bang and Bang 1959; Moore 1981). Significantly, in birds, too, the olfactory posterior turbinal is usually positioned outside the respiratory airstream, and may even be situated in a blind recess in forms with a well-developed sense of olfaction (Fig. 7).

Embryonically, the conchae and turbinals of all higher tetrapods develop from folds of the cartilaginous nasal capsules (Goodrich 1930; Matthes 1934; Parsons 1970; Moore 1981). The homologies of these structures in the various groups are, however, uncertain (De Beer 1937; Hyman 1942; Parsons 1970; Moore 1981) even between closely related groups with apparently similar nasal configurations, such as crocodiles and birds (e.g., Parsons 1970). Much of the evidence used to determine these relationships is ambiguous and contradictory. The mammalian maxilloturbinal is usually considered to be homologous to the main reptilian concha (e.g., Kingsley 1926; Allison 1953; Parsons 1970; Moore 1981). This implies that mammalian ethmoturbinals evolved later, after the divergence of reptiles and mammals. Ontogenetically, however, the maxilloturbinals develop later than the ethmoturbinals (Parker 1907; Matthes 1934; Roux 1947; Jollie 1968; cf. Miao 1988), suggesting the ethmoturbinals are phylogenetically more ancient. The latter scenario seems more reasonable when the functions of the turbinates, as well as their fossil record, are considered.

Turbinates and endothermy

Several authors have suggested that nasal turbinate function is correlated with endothermy, at least in mammals and their ancestors (e.g., Watson 1913, 1951; Brink 1955, 1956; Van Valen 1960; Bennett and Ruben 1986). However, since the turbinates of mammals perform several distinct functions, their relationship to endothermy is not straightforward in every case. According to Bennett and Ruben (1986), a structure is diagnostic of endothermy only if it has a clear, and exclusive, functional association with high metabolic rates, and is not present in ectotherms. These conditions are met by the respiratory maxilloturbinals, whose function is clearly correlated with the elevated pulmonary ventilation rates of mammals (Hillenius 1992). Because of these high ventilation rates, respiratory water loss is potentially a more serious problem for mammals than for reptiles, and the need for water loss reduction is more compelling. Complex maxilloturbinals, covered with mucociliated epithelium, enable mammals to recover a substantial portion of the water contained in exhaled air (Collins et al. 1971; Hillenius 1992), and these structures very likely evolved in concert with the development of elevated ventilation rates (Hillenius 1992). None of the much less elaborate reptilian conchae seem likely to have a significant respiratory function. However, the respiratory turbinals of birds (Fig. 7) also appear to

be capable of reducing respiratory water loss (Schmidt-Nielsen et al. 1970; Berger et al. 1971; Murrish 1973), and may represent an adaptation to high ventilation rates analogous to the mammalian maxilloturbinal.

For the other mammalian turbinates, however, there is no particular correlation with endothermy. While the ethmoturbinals are far more complex and extensive than reptilian conchae, they retain the same sensory function. Their increased complexity in mammals probably reflects the greater olfactory acuity of these animals (Matthes 1934; Parsons 1971; Romer and Parsons 1986). An indirect relationship with high ventilation rates may possibly exist, however, as the shape and orientation of the ethmoturbinals appear to help protect the olfactory epithelium from exposure to strong air currents. Nevertheless, at this time not enough is known about the effect of strong air currents on olfactory epithelium to support a close functional association between these turbinals and endothermy.

The function of the nasoturbinal is the least consistent among mammals, and its relationship with endothermy the most ambiguous. Although it bears olfactory epithelium posteriorly, the anterior portion is usually covered with respiratory epithelium. In some small rodents and insectivores, which have relatively small maxilloturbinals, the nasoturbinal may be as important as the maxilloturbinal in modifying respired air and reducing respiratory water loss (Adams 1972; Woehrmann-Repenning 1975; Popp and Martin

1984). In these animals, the nasoturbinal may be scrolled or even branched (Fig. 9). However, in most other mammals the nasoturbinal is much less extensive than the maxilloturbinal, consisting only of a simple lamella (Fig. 9). Here, its contribution to respiratory water loss reduction is probably negligible. Instead, the nasoturbinal appears to serve primarily as a baffle to guide a sample of inhaled air toward the olfactory region during sniffing. As mentioned above, the nasoturbinal is often considered one of the ethmoturbinals; it may have extended forward to allow air samples to bypass the maxilloturbinal. In this case, the secondary replacement of sensory by respiratory epithelium may relate simply to exposure to high air currents, in which sensory cells may not operate effectively. A similar retreat of sensory epithelium is occasionally seen on the rostral tips of the ethmoturbinals, where these dip into the airstream (e.g., Dodd and Squirrell 1980).

In summary, of the mammalian nasal turbinates, only the maxilloturbinal shows a clear functional relationship to endothermy. Its main function appears to be to reduce potentially high respiratory water loss rates associated with elevated ventilation rates. Conversely, the mammalian ethmoturbinals retain the primitive olfactory function of the nasal conchae, although their increased complexity in mammals might be correlated to high air current velocities. The nasoturbinal probably represents a forward extension of

the ethmoturbinals, which guides air toward the olfactory region. In certain small mammals, the nasoturbinal may, in addition, aid the maxilloturbinal in its respiratory functions. Avian turbinals probably have respiratory and olfactory functions analogous to those of mammals.

Turbinates in the fossil record

Preservation of turbinates

The fragility of turbinates usually precludes their preservation in fossilized specimens. Moreover, they may have been cartilaginous in early stages of their evolution, as they are in extant reptiles and birds. In most cases, the best evidence for their presence in fossil taxa are the basal ridges by which the turbinates attach to the lateral walls of the nasal cavity (Watson 1913; and many others since then).

These basal ridges form a characteristic pattern in extant mammals (Fig. 8b). The ethmoturbinals are supported by a series of more or less parallel ridges, usually located on the ventro-medial surfaces of the the frontal bone. These ridges extend from the level of the anterior edge of the transverse lamina, and terminate at the cribriform plate of the ethmoid. The most dorsal of these ridges continues anteriorly onto the nasal, and supports the nasoturbinal. Occasionally the nasoturbinal is supported by two closely parallel ridges (Fig. 8b), separated by a narrow canal which conveys blood vessels. Finally, the maxilloturbinal is supported by a separate ridge, which is situated in the anterolateral portion of the nasal cavity, apart from the others. It is usually located on the ascending process of

the maxillary, but may be partially or entirely located on the premaxillary bone (e.g., in rodents and lagomorphs).

The locations of these basal ridges reflect the functions of the turbinals as well. The ridges of the olfactory ethmo- and nasoturbinals are restricted to the posterodorsal portions of the nasal cavity, above the transverse lamina, and away from the respiratory pathway. In contrast, the ridge of the maxilloturbinal is located in the respiratory passage, anterior to the transverse lamina (Fig. 8b).

The maxilloturbinal ridge is also situated in close proximity to the ostium of the the nasolacrimal duct (Fig. 8b). In life, the duct continues forward along the base of the turbinal (Fig. 9) to its opening in the floor of the nostril, near the anterior part of the maxilloturbinal (Evans and Christensen 1979; Nickel et al. 1979). This close association between the nasolacrimal duct and the maxilloturbinal occurs in all mammals in which the duct is present, and suggests a functional relationship between these two structures. Several authors indicate that exudate from the nasolacrimal duct may contribute to the moistening of inhaled air, and facilitate the operation of the maxilloturbinal system (Bojsen-Moller 1964; Nickel et al. 1979; Romer and Parsons 1986).

Early Mammals

The pattern of attachment ridges for the turbinates appears essentially uniform in all extant mammals. The same basic pattern is also evident in early mammals, although few descriptions of their nasal cavities are available.

A complex series of anteroposteriorly oriented ridges has been described in the nasal cavities of the late Paleocene multituberculate Lambdopsalis (Miao 1988), and of Morganucodon, one of the oldest known mammals from the Late Triassic and Early Jurassic Periods (Kermack et al. 1981). In both forms, ridges are present dorsally, on the inner surfaces of the nasal and frontal bones, as well as laterally, on the ascending process of the maxillary. The arrangement of these ridges closely resembles the typical mammalian pattern, and indicates that both respiratory and olfactory turbinates (i.e. maxilloturbinals, and naso- and ethmoturbinals) were present in life. The course of the nasolacrimal duct is not described in Lambdopsalis, but in Morganucodon a groove on the ascending process of the maxillary suggests that it lies at the base of the maxilloturbinal, as in modern mammals (Kermack et al. 1981).

Ossified turbinates are actually preserved in the Late Jurassic docodont Haldanodon (Lillegraven and Krusat 1991). Remnants of maxilloturbinals and ethmoturbinals, which indicate that these structures were quite extensive and complex, are described in a number of specimens. Typical

mammalian turbinal attachment ridges occur on the maxillary, nasal and frontal bones. However, the authors indicate the presence of several additional ridges on the ascending process of the maxillary, supporting a complex series of maxilloturbinal elements (Lillegraven and Krusat 1991, p. 62). This appears to differ from the situation in other mammals, where the maxilloturbinal always arises from a single base, regardless of its subsequent complexity (see Fig. 9). The significance of the condition in Haldanodon is not clear. The course of the nasolacrimal duct in Haldanodon is comparable to modern mammals, ventral to the attachment of the maxilloturbinal complex (Lillegraven and Krusat 1991).

Multituberculates and docodonts diverged from the other lineages early in mammalian evolution (Kron 1979; Clemens and Kielan-Jaworowska 1979; Miao 1988; Lillegraven and Krusat 1991), while morganucodontids are thought to occupy a position near the base of the mammalian phylogeny (Crompton and Jenkins 1979; Hopson 1987; Rowe 1988; Wible et al. 1990). The presence in these animals of an essentially mammalian turbinal complex, inclusive of extensive respiratory maxilloturbinates, strongly indicates that even the earliest mammals possessed high ventilation and oxygen consumption rates, similar to those of modern mammals. Most authors, in fact, agree that endothermy was most likely a primitive feature of mammals (McNab 1978; Bennett and Ruben 1986; Hopson 1987; Carroll 1988; Jenkins 1990).

Pelycosaurs

Among the reptilian ancestors of mammals, turbinal ridges appear to go back as far as early pelycosaurs, the oldest (Late Carboniferous and Early Permian Period) and most primitive group of synapsid reptiles (Fig. 11). Romer and Price (1940) describe such ridges in both Ophiacodon, a primitive pelycosaur, and Dimetrodon, a more advanced form, and presume they were probably present in other forms as well. The ridges are located in the posterodorsal corner of the nasal cavity, in a preorbital recess, and radiate fanwise over the prefrontal (Fig. 12). Romer and Price (1940, p. 58) suggest the ridges themselves represent incipient turbinals; alternatively they may have supported more extensive turbinals which were not preserved. In either case, the posterodorsal location of these ridges indicates that their function was most likely olfactory. Further evidence for this is provided by the sphenethmoid bone (Reisz 1986; the "presphenoid" of Romer and Price 1940), which is located immediately behind the level of the ridges (Fig. 12). This median bone separates the nasal and cerebral cavities, and contains a number of foramina through which olfactory nerves pass. The ridges on the prefrontal converge toward these foramina, as if their associated structures received olfactory sensory innervation.

Romer and Price (1940) also describe a pair of longitudinal grooves on the ventral surface of the nasal and

frontal bones. These grooves appear situated on a pronounced ridge, which extends anteriorly from the orbits (Fig. 12). The grooves are interpreted as marking the edges of the cartilaginous internasal septum (Romer and Price 1940, p. 57). However, the comments of Tatarinov (1963) may also apply here: the distance between these grooves or ridges would indicate an extraordinarily thick nasal septum. In modern mammals and reptiles, the septum is a thin structure which attaches to a slight mid-dorsal ridge, rather than a wide groove. Furthermore, the nasoturbinal ridges of modern mammals are often grooved to provide space for bloodvessels (see Fig. 8b), and their location generally corresponds with that of the grooved ridges in pelycosaurs. It is therefore possible that the grooved ridges of pelycosaurs similarly supported nasoturbinals, rather than an internasal septum. Like the turbinals of the prefrontals, however, these would have been primarily olfactory in function.

In contrast, no turbinal ridges are found in the respiratory portion of the nasal cavity. The course of the nasolacrimal duct within the nasal cavity is indicated in Dimetrodon by a shallow groove which continues from the anterior end of the lacrimal bone to the septomaxillary (Fig. 12). No ridges are associated with this groove. The respiratory passage of pelycosaurs is relatively short despite the large size of their nasal cavity, because the internal nares are located far forward, as is typical for

primitive tetrapods. In Dimetrodon the palate closes just behind the canines (Fig. 12), forcing respired air into the oral cavity at this level. Consequently, little space is available for nasal modification of respired air. Lack of turbinal ridges in this area also suggests that recovery of respiratory water was not a great priority for these animals, and it seems unlikely that their ventilation rates had expanded beyond those of typical reptiles. This is in accordance with the conventional view of pelycosaurs as "typical reptilian ectotherms" (Bramwell and Fellgett 1973; Bakker 1975; Kemp 1982; Turner and Tracy 1986; Haack 1986; Carroll 1988).

Primitive Therapsids

Among primitive therapsids, Orlov (1958) describes longitudinal ridges on the ventral surface of the nasal and frontal bones of the Upper Permian dinocephalian Titanophoneus, but interprets these as marking the lateral edges of the nasal septum. Tatarinov (1963) disagrees, however, and considers the ridges turbinal supports instead. The distance between the ridges would have resulted in an exceptionally thick nasal septum. Furthermore, Tatarinov (1963) points out that the ridges figured by Orlov are grooved, and are comparable to paired nasoturbinal ridges found in more advanced therapsids and mammals. Longitudinal nasofrontal ridges also appear to be present in the titanosuchid dinocephalian Jonkeria (Boonstra 1968). However, in both animals, the posterodorsal location of the ridges indicates that their function was most likely olfactory. No ridges have been described for respiratory portion of the nasal cavities of Titanophoneus or Jonkeria, which, like that of pelycosaurs, was restricted by the anterior location of the primary palate.

Dicynodonts

Among dicynodonts, longitudinal nasofrontal ridges are known in several genera (Lystrosaurus, van Hoepen 1913; Cluver 1971; Pristerodon, Barry 1967; Kingoria, Kemp 1969). These ridges have been associated with the sphenethmoid complex by some (Barry 1967; Cluver 1971), but are interpreted by others as turbinal ridges (Kemp 1969, 1982; Cluver 1971). In both Lystrosaurus and Pristerodon the ridges are paired, and closely resemble the nasoturbinal ridges of other therapsids (Fig. 13). In addition, in Pristerodon a short ridge is present in a preorbital recess of the nasal cavity, lateral to the nasoturbinal ridges (pers. obs.), which indicates the presence of an ethmoturbinal. The posterodorsal, interorbital location of all these ridges suggests that their function is almost certainly olfactory.

Dicynodonts are the first group of therapsids to develop a secondary palate. This feature has been linked to endothermic physiology (Brink 1956; Parrington 1967; McNab 1978), as it permits uninterrupted breathing during mastication, and its presence in dicynodonts has been considered suggestive of endothermy (King 1990). As Bennett and Ruben (1986) point out, however, a secondary palate also occurs in a number of extant reptiles, which makes this feature by itself a poor indicator of metabolic status. Thomason and Russell (1986) suggest that the secondary

palate evolved primarily for structural considerations. In the case of dicynodonts, Kemp (1982) considers the secondary palate too closely associated with their peculiar feeding mechanism to reveal anything about their metabolic rates. Furthermore, the short snout of dicynodonts (King 1981) would tend to negate any increase in the size of the nasal respiratory chamber like that which accompanies the development of the secondary palate in more advanced therapsids (discussed below). No lateral ridges, indicative of possible respiratory turbinates, have been described in dicynodonts, and there is no evidence to suggest that their secondary palate was accompanied by elevated ventilation rates. The course of the nasolacrimal duct is known in Lystrosaurus, where it is clearly marked by a shallow sulcus between the ostium of the lacrimal canal and the septomaxillary canal (Fig 13; Cluver 1971). A similar course is suggested by Cox (1959), for Kingoria. In either case, however, no ridges are associated with this sulcus.

Gorgonopsians

The nasal cavity of gorgonopsians is much larger than in dicynodonts, but, like pelycosaurs, and other primitive therapsids, they lack a bony secondary palate. Some authors suggest that a membranous secondary palate may have existed in gorgonopsians (Watson 1921; Kermack 1956; Tatarinov 1963; Kemp 1982), others consider this unlikely (Kemp 1969; Sigogneau-Russell 1989). The internal nares of gorgonopsians are situated in the anterior half of the palate, and the respiratory passage is therefore still relatively short. The largest portion of the nasal cavity, located behind the level of the posterior margin of the internal nares, was most likely dedicated primarily to olfaction. According to Kemp (1969), a transverse choanal process rose from the posterior margin of the internal nares into the nasal cavity, like a bulkhead, and restricted access to this olfactory chamber. A similar structure was, however, not observed by Sigogneau-Russell (1989).

A number of longitudinal ridges occur in the gorgonopsian nasal cavity, which are interpreted as turbinal ridges (Kemp 1969). Two pairs of closely parallel ridges occur along the ventral surface of the nasal and frontal bones, one pair on either side of the midline (Fig. 14). These are similar to ridges observed in other therapsids, and to the ridges that support the nasoturbinals of extant mammals. One or two additional ridges are located

posterolateral to these, in the preorbital olfactory recess, which closely resemble ethmoturbinal ridges (compare Fig. 8b). The function of these structures was most likely olfactory. Finally, in Arctognathus, a pair of ridges is located in the ventral portion of the nasal cavity, in the maxillary sinus. Because these ridges are found on the ascending process of the maxillary bone, Kemp (1969) suggests they may have supported maxilloturbinals. However, these ridges are located behind the internal nares and the transverse choanal process, and it is unlikely that they were involved in modification of respiratory air, as is the case with the maxilloturbinals of modern mammals. Instead, they were more likely olfactory; their presence in a cranial sinus is reminiscent of a similar condition in some mammalian carnivores. No ridges have been described that suggest the presence of respiratory turbinates in gorgonopsians.

The large number of olfactory turbinals in gorgonopsians suggests that these animals had a comparatively well developed olfactory sense, but says little about their ventilation rates. The presence of a transverse choanal process in some forms, which would restrict air circulation in the olfactory chamber, and the location of some of the olfactory turbinals in a protected maxillary sinus, may possibly indicate that ventilation rates had increased enough to begin to have a deleterious effect on the olfactory epithelium, thus requiring such protective

measures. However, there is, so far, no direct evidence to suggest that ventilation rates had increased to a point where reduction of respiratory water loss became necessary.

Kemp (1969) concluded that the gorgonopsian nasolacrimal duct passed through the maxillary sinus, and opened ventrally into the choana. However, in several broken snouts of gorgonopsians at the South African Museum (e.g., SAM K8790 and SAM K10054), the nasolacrimal duct has a more dorsal location, and appears to maintain an essentially horizontal course toward the anterior nasal cavity (pers. obs.).

Therocephalians

Both remaining groups of therapsids, the therocephalians and the cynodonts, became increasingly mammal-like in appearance during the course of their evolution. Their vertebral column became differentiated into cervical, thoracic and lumbar regions, and the appendicular skeleton of both groups suggests an increased reliance on erect, rather than sprawled, gait (Jenkins 1970, 1971; Kemp 1978, 1986). Their dentition became increasingly complex, and both therocephalians and cynodonts eventually developed a complete bony secondary palate (Kemp 1982). Although the cynodonts, which outlived the therocephalians after the Early Triassic, continued this trend much further, and ultimately gave rise to the first mammals (Fig. 11), both groups are suspected of having been more "mammal-like" than previous therapsids in their physiology and metabolic status (Van Valen 1960; McNab 1978; Kemp 1982).

Among therocephalians, turbinal ridges have been noted along the roof of the nasal cavities of Akidnognathus (Brink 1960) and Moschowhaitsia (Tatarinov 1963). These are similar to the nasofrontal ridges found in other therapsids, and to the ridges of the mammalian nasoturbinals. As indicated by their dorsal location, they most likely had an olfactory, rather than a respiratory, function. Previously, no ridges for potential respiratory turbinals have been described for therocephalians.

However, in a specimen of the primitive therocephalian Glanosuchus (GS M796), an additional ridge occurs ventral to the nasoturbinal ridge, on the lateral wall of the nasal cavity (Fig. 15). The location of this ridge suggests it may have supported a respiratory turbinal. It is formed by the ventral edge of the nasal bone, which projects into the nasal cavity along its contact with the maxilla. Although it forms only a slight ledge, it is unlikely that this ridge is an artifact of distortion or dislocation. While in many therapsid fossils the nasal bones have frequently been dislocated as a result of dorsoventral compression of the nasal cavity, there is no evidence of such dislocation in GS M796. The specimen has suffered some lateral compression, but compressional distortion is limited primarily to the mid-sagittal portions of the skull roof and the palate. Other portions are remarkably free of distortion, and the entire lateral part of the skull, including the nasal-maxillary contact, is essentially intact.

The ridge in GS M796 is situated anterior to the level of the primary palate (Fig. 15), and thus remains in the respiratory portion of the nasal cavity. It is located well below the clearly recognizable nasoturbinal ridge, and immediately anterior to the anterior process of the lacrimal, which introduces the nasolacrimal duct into the nasal cavity (Fig. 15). In life this duct probably continued anteriorly to the septomaxilla, to open in or near the external nares. The ridge in GS M796, therefore, lies

closely dorsal to the likely course of the nasolacrimal duct, similar to the respiratory turbinal of modern mammals.

In extant mammals, the only structures associated with ridges in the lateral portion of the nasal cavity are the respiratory maxilloturbinal and the nasolacrimal duct (Fig. 8). Although in adult mammals this turbinal is generally attached to the maxillary bone, rather than the nasal, it develops ontogenetically from a distinct cartilaginous precursor, which only later becomes attached to the adjacent dermal bones (Moore 1981). As a result, the location of the basal attachment of the maxilloturbinal is relatively flexible, and varies considerably among mammals (Fig. 9). It may even be located on the premaxillary, e.g. in rodents and lagomorphs. It is therefore entirely possible that this turbinal attached to the ventral portion of the nasal in therocephalians.

Additional ridges, which most likely supported olfactory turbinals, are present elsewhere in the nasal cavity of Glanosuchus. The nasoturbinal ridge has already been mentioned. It stretches anteriorly from the interorbital region, along the ventral surfaces of the frontal and the nasal bones (Fig. 15). As in many other therapsids, its posterior half consists of two closely parallel ridges, separated by a narrow groove. Anteriorly, the nasoturbinals become less pronounced. At least two other ridges are present posteriorly in the preorbital recess of the nasal cavity (Fig. 15). These are located on the frontal and

prefrontal bones, lateral to the posterior part of the nasoturbinal ridge, and correspond to the ethmoturbinal ridges of other therapsids and extant mammals. The inner surface of the prefrontal is damaged in this area, so the exact number of these ridges cannot be determined. There is no evidence of turbinal ridges in the maxillary "sinus."

The presence of possible respiratory turbinal ridges in Glanosuchus suggests that its nasal cavity had become actively involved in the conditioning of respired air, and suggests that the ventilation rate of this animal had increased enough to result in significant respiratory water loss. However, Glanosuchus also retains the primitive reptilian palate, where the anterior location of the internal nares limits the size of the nasal respiratory chamber (Fig. 15). Consequently, its capacity to recover respiratory water vapor was probably limited as well, which suggests that the increase in the ventilation rate of this early therocephalian was likely to have been relatively modest. Nevertheless, as Glanosuchus dates from the middle Late Permian, about 260 million years ago (Van den Heever 1987), this marks the earliest indication that the ventilation rates of advanced therapsids had expanded over ancestral "reptilian" rates.

It is not known at present whether other therocephalians possessed respiratory turbinals. However, the nasal respiratory chamber of therocephalians gradually expanded over the course of their evolution, as indicated by the

progressive posterior migration of the internal nares (Fig. 16). As a result, more space became available for conditioning respiratory air, and recovery of water vapor. This suggests that ventilation rates may have been gradually expanding during therocephalian evolution, which is consistent with the increasingly mammal-like composition of this group.

Cynodonts

Cynodonts supplanted the gorgonopsians and therocephalians as the dominant therapsids during the Early Triassic Period (Kemp 1982; Carroll 1988), and persisted throughout the Triassic, and into the Jurassic (Fig. 11). During this period, their morphology increasingly approached the mammalian condition. Of all therapsids, the cynodonts acquired the greatest number of mammalian features, and the most advanced cynodonts ultimately gave rise to the first mammals (Hopson and Barghusen 1986; Rowe 1988). Because of the progressively mammalian appearance of this group, many authors have speculated that cynodonts had acquired a mammal-like, endothermic physiology as well (Watson 1951; Brink 1956; Van Valen, 1960; Parrington 1967; Hopson 1973, 1987; McNab 1978; Bennett and Ruben 1986).

Longitudinal turbinal ridges have been noted on the inner surfaces of the nasal, frontal and prefrontal bones of many cynodonts (Procynosuchus, Kemp 1980; Thrinaxodon (incl. "Nythosaurus"), Watson 1913; Fourie 1974; Diademodon, Watson 1913; Brink 1955, 1956; Exaeretodon, Bonaparte 1966; Luangwa, Kemp 1979; Oligokyphus, Kuehne 1956). Several authors have referred to these ridges as evidence for cynodont endothermy (eg. Watson 1951; Brink 1956; Bennett and Ruben 1986). However, these ridges do not differ from those of earlier therapsids, and correspond to the ridges that support the olfactory ethmo- and nasoturbinals of

extant mammals. Their posterodorsal location makes it unlikely that they had a respiratory function. Consequently, these turbinal ridges provide little insight into the metabolic status of cynodonts.

However, in several cynodonts, ridges do occur in the anterolateral portion of the nasal cavity, which have not been described previously. These ridges correspond in location to the maxilloturbinal ridges of extant mammals, and are similar to the ridge for the respiratory turbinal of Glanosuchus, described above. In at least two specimens of the Middle Triassic gomphodont Massetognathus (MCZ 4219 and MCZ 4240), a pronounced ridge is present ventral to the nasoturbinal ridge, in the anterior portion of the nasal cavity (Figs. 17, 18). As in Glanosuchus, the ridge is formed by the ventral edge of the nasal bone, which forms a distinct ledge into the nasal cavity. In both specimens, the ridges appear to be a natural feature, and are unlikely to be the product of preservational distortion. Neither specimen has suffered any noticeable dorsoventral compression, and the bones surrounding the snout are essentially intact. In MCZ 4240, which consists of a series of transverse sections, the nasals of both sides project inward symmetrically (Fig. 17).

As in the therocephalian Glanosuchus, the ridges in Massetognathus are situated within the respiratory chamber, in front of the primary palate (Fig. 18). They are located directly anterior to the ostium of the nasolacrimal duct,

and trace the probable course of the nasolacrimal duct to the rostral portion of the snout. In MCZ 4219, the anterior portion of the snout is missing, but in MCZ 4240, the projection of the nasals can be followed to the point where these bones meet the septomaxillae.

Additonally, the nasal bones of Massetognathus extend farther ventrally than in Glanosuchus, so that their lower edges are situated near the center of the lateral wall of the nasal cavity (Figs. 17, 18). As a result, these ridges more closely match the typical position of the base of the mammalian maxilloturbinal (Fig. 8b, 9).

Similar ridges also occur in a specimen of Trirachodon (NMB QR3268), and in two acid-prepared specimens of Thrinaxodon (AMNH 2226 and an uncatalogued specimen at the MCZ). These are both Early Triassic forms. The ridges are somewhat less pronounced in Thrinaxodon, but in both genera, the position of these ridges, and their relation to the ostium of the nasolacrimal duct, are identical to those in Massetognathus. None of these specimens show any distortion in the snout area.

The nasoturbinal ridges in Massetognathus are largely similar to those in other cynodonts. Posteriorly, these ridges show a shallow groove. In MCZ 4219, a number of ethmoturbinal ridges are present on the prefrontal and the orbital process of the lacrimal (Fig. 17).

The ridges in the anterolateral portion of the nasal cavities of Massetognathus, Trirachodon and Thrinaxodon

closely resemble the basal ridge of the mammalian maxilloturbinal. Their location in the large respiratory chamber, and their association with the nasolacrimal duct strongly suggest that these ridges supported a turbinal structure like that found in extant mammals, with a similar water-recovery function. This provides compelling evidence that ventilation rates of these cynodonts were elevated significantly above "reptilian" rates, and may perhaps have approached the "mammalian" level.

Summary and Conclusions

Nasal turbinates are a useful, and rigorous indicator of the metabolic status of extinct vertebrates, as has been suggested by Watson (1951), Brink (1956) and Bennett and Ruben (1986), provided a distinction is made between olfactory and respiratory elements. Respiratory turbinals are found only in mammals and birds, and their function, at least in mammals, but probably in birds as well, is to reduce the respiratory water losses associated with rapid and continuous pulmonary ventilation, a fundamental component of endothermic physiology (Hillenius 1992). The respiratory turbinals, therefore, satisfy Bennett and Ruben's (1986) criteria for a diagnostic character of endothermy. This is not the case for olfactory turbinals, however, which retain the primitive function of the reptilian nasal conchae. Their increased complexity in endotherms is most likely a reflection of the greater olfactory acuity of these animals.

Although the fragile nasal turbinates are rarely preserved in fossils, their presence, as well as their function, is revealed by characteristic ridges on the walls of the nasal cavity, to which the turbinates attach. In mammals, the olfactory naso- and ethmoturbinals attach to ridges in the dorsal and posterior portions of the nasal cavity, away from the path of respired air. Alternately, the respiratory maxilloturbinals are suspended from a ridge

with an anterolateral location, within the respiratory passage. In addition, the respiratory turbinals of mammals are closely associated with the ostium of the nasolacrimal duct. There appears to be a functional relationship between the maxilloturbinal and this duct, which provides some of the moisture required to operate the turbinal complex.

Examination of the nasal cavities of the ancestors of mammals, the synapsid reptiles, indicates that olfactory turbinals were very likely present at an early stage, among the earliest forms to diverge from the main reptilian lineage, and well before endothermy was likely to have evolved. Ridges along the dorsal and posterolateral walls of the nasal cavities of ophiacodont and sphenacodont pelycosaurs resemble those of the olfactory naso- and ethmoturbinals of extant mammals. Similar ridges are also found throughout the therapsids, the descendants of pelycosaurs. Although these ridges have frequently been cited as evidence of therapsids endothermy, in reality they reveal little about the animals' metabolic status.

Ridges probably associated with respiratory turbinals first appear among advanced therapsids, the therocephalians and cynodonts (see Appendix B for list of specimens). These ridges closely resemble the mammalian maxilloturbinal ridges in their anteroventral location, within the respiratory chamber, and in their association to the ostium of the nasolacrimal duct. They differ from the mammalian ridges in that they are located on the ventral border of the nasal

bone, rather than the maxilla. However, since the maxilloturbinal develops ontogenetically from a separate precursor, and the position of its basal attachment site varies considerably among extant mammals, this variation is probably insignificant. In all specimens in which this ridge has been described, it appears to be a natural feature, and not an artifact of preservation.

The pattern of nasal turbinal ridges in therapsids indicates that the ventilation rates of the more primitive groups (dinocephalians, dicynodonts and gorgonopsians) probably had not yet increased significantly beyond ancestral rates. Although their limb suspension was more advanced, and their posture more erect than in pelycosaurs (see Kemp 1982), suggesting a somewhat more active lifestyle, physiologically, these animals probably remained within the realm of ectothermy. However, the maxilloturbinal ridges in therocephalians and cynodonts suggest that ventilation rates in these taxa had increased substantially. This is the first clear sign that the evolution of endothermy had begun.

Presently, the earliest evidence for elevated respiration rates is found in Glanosuchus, a primitive therocephalian of the middle Late Permian (approx. 260 million years ago). In this form, respiratory turbinals occur in combination with an essentially reptilian palatal configuration, which limits the nasal respiratory chamber, and, most likely, its capacity to modify respiratory air.

This suggests that while the respiration rates of early therocephalians had already increased sufficiently beyond "reptilian" rates to cause significant respiratory water loss, progress towards "mammalian" levels of respiration was still relatively modest. In later therocephalians, the nasal respiratory chamber gradually expanded (Fig. 16), suggesting that their ventilation and metabolic rates were gradually increasing as well.

Cynodonts were closely related to therocephalians, which they superseded during the Early Triassic, but the two groups apparently diverged early in their phylogenetic history (Kemp 1982; Hopson and Barghusen 1986). Many of the mammal-like features found in both groups, such as the secondary palate and the differentiated vertebral column, clearly developed independently. If early therocephalians possessed only moderately elevated ventilation rates, the same was likely also true for the first cynodonts. Consequently, the expansion of the aerobic capacity of both groups probably progressed largely in parallel as well.

Throughout their evolution, cynodonts progressively acquired additional mammalian characters, and their morphology was gradually transformed from generally reptile-like, to very mammal-like. Modifications of their appendicular skeleton indicate that the locomotory capabilities of cynodonts steadily improved (Jenkins 1971), while changes in dentition and the structure of the lower jaw suggest that the rate of food assimilation increased

(Kemp 1982). Although individually, these features may have little direct bearing on the development of endothermy (Bennett and Ruben 1986), collectively they suggest that the metabolic capacities of cynodonts were steadily expanding. This is strongly supported by the presence of ridges for respiratory turbinals in at least three cynodont taxa, which indicate that the ventilation and concomitant respiration rates of these animals were indeed significantly increased. The fact that these mammalian characters were accumulated gradually over time indicates that the attendant physiological processes probably changed in a gradual fashion as well.

Ultimately, cynodonts gave rise to the first mammals by the end of the Triassic Period (approx. 215 million years ago). The nasal turbinal ridges of the earliest mammals are essentially identical to those of extant mammals, suggesting that the development of "mammalian" respiration rates, and endothermy, was largely complete by this time (c.f., Bennett and Ruben 1986; Jenkins 1990; Bennett 1991). Consequently, between the Late Permian and the Late Triassic, the process of the evolution of endothermy may have required as much as 40 to 50 million years.

In conclusion, two main theories have been advanced regarding the selective factors behind the evolution of endothermy. In the first scenario, high resting metabolic rates developed to facilitate metabolically-based thermoregulation, and the maintenance of a constant body

temperature independent of environmental temperature fluctuations. (e.g., Crompton et al 1978; McNab 1978; Taylor 1980). However, Bennett (1991) points out that metabolic heat production at most levels intermediate between reptiles and mammals is insufficent to establish endothermic homeothermy, and thus provides little thermoregulatory benefit, but would substantially increase the animal's energy budget. Given the long time period apparently involved in the evolution of endothermy, it is unlikely that homeothermy was a significant selective factor in this process. The present findings of slow development of mammalian metabolic rates are more consistent with the second theory, the aerobic capacity model, which invokes the advantages of an increased capacity for sustained, aerobically supported activity (Bennett andd Ruben 1979; Hopson 1987; Bennett 1991). Here, even very modest increases in metabolic rate directly expand endurance, and normal activity levels. Thus, aerobic capacities and stamina of therocephalians and cynodonts could have expanded very gradually, without resultant adaptive "valleys."

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Figure 6. The reptilian nasal cavity. A. Lacerta, right sagittal section (after Matthes 1934). B. Alligator, right sagittal section. C. Cross-sections through the concha of Lacerta (after Matthes 1934), and the middle concha of Alligator. For abbreviations, see p. 135.

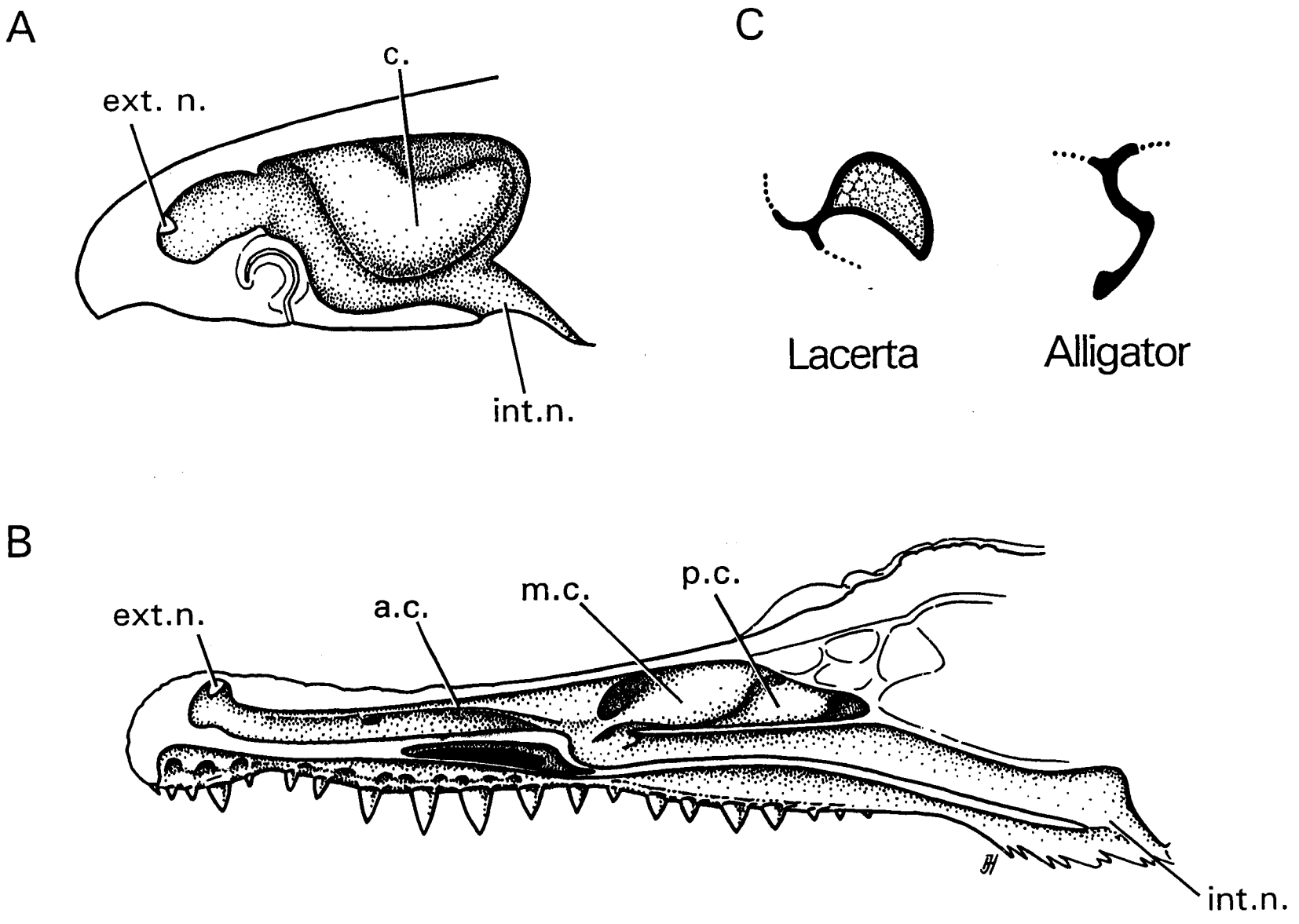
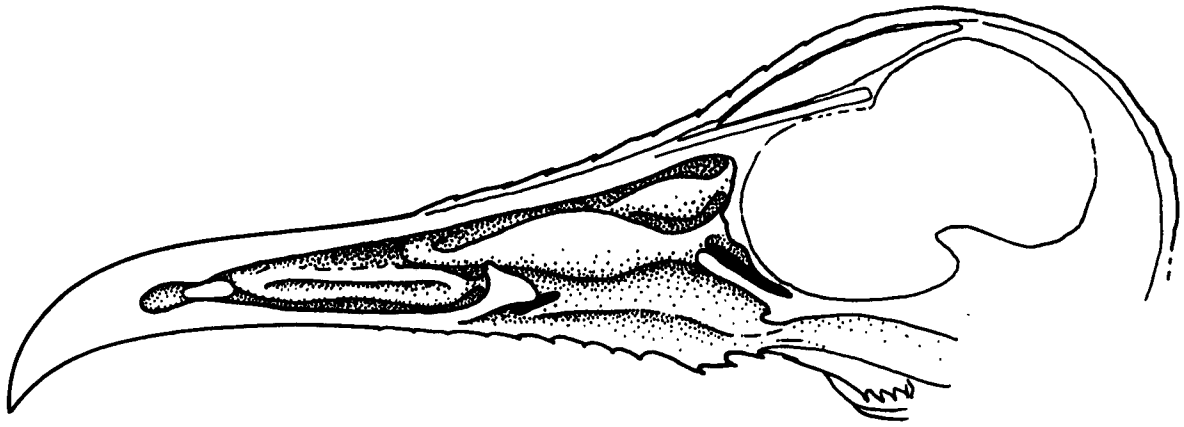

A
c.
ext. n.
int.n.
C
Lacerta
Alligator
B
ext.n.
a.c.
m.c.
p.c.
int.n.

Figure 7. The avian nasal cavity. A. Larus, right sagittal section (after Bang 1961). B. Cross-sections through the middle (respiratory) turbinals of Coragyps (after Bang 1964), Fulmarus (after Bang 1968), Rhea and Dromaius (after Bang 1971). For abbreviations, see p. 135.

A

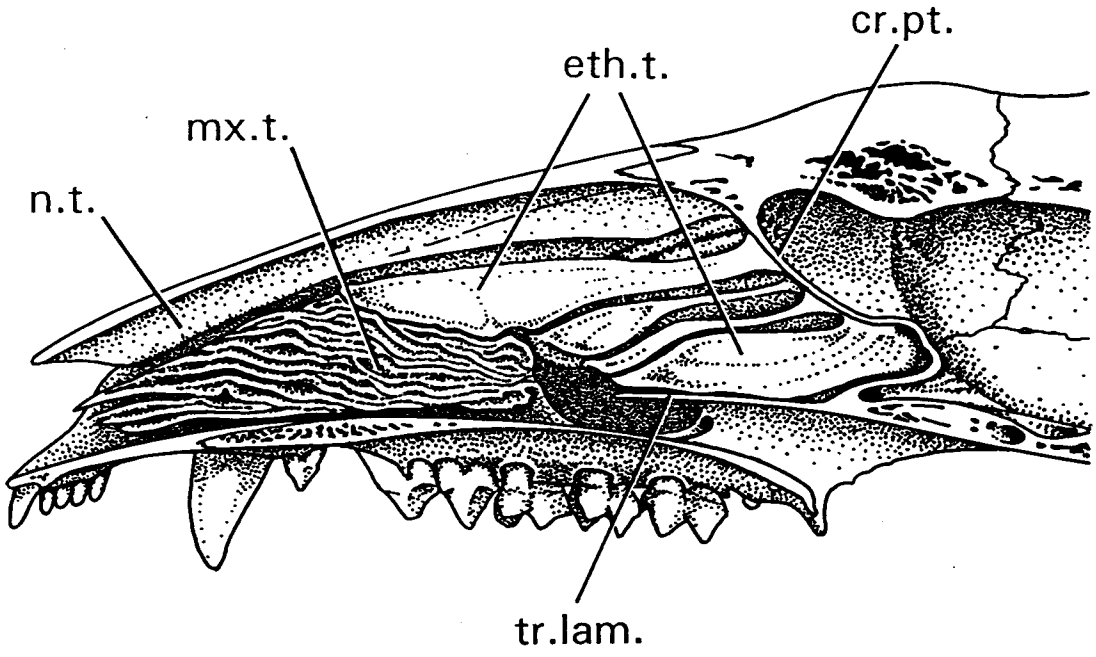


B

Coragyps Fulmarus Rhea Dromaius

Figure 8. The mammalian nasal cavity. A. Didelphis, right sagittal section. B. Similar, but with the turbinates removed to reveal the turbinate attachment ridges. For abbreviations, see p. 135.

A



B

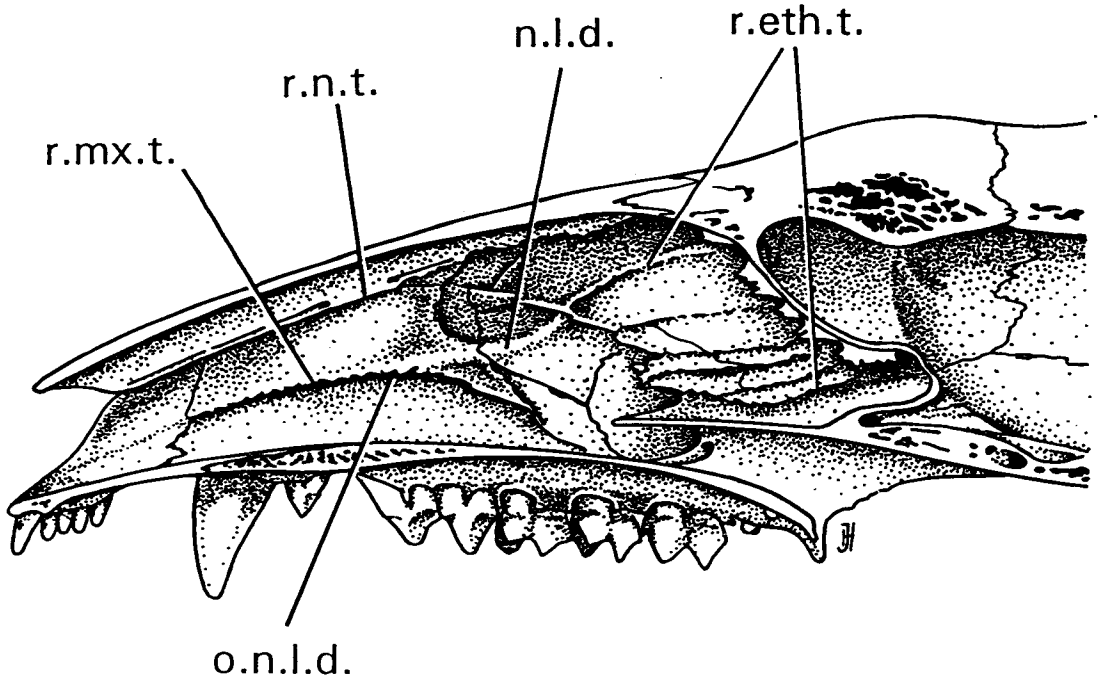


Figure 9. Cross-sections through the anterior nasal turbinals of several mammalian species. Homo (after Negus 1958), Syncerus (original), Meles (after Anthony and Iliesco 1926), Phoca (after Negus 1958), Caenolestes (after Broom 1926), Dipodomys (after Bang and Bang 1959), Peromyscus (after Adams 1972), Sorex and Erinaceus (after Woehrmann-Repenning 1975). For abbreviations, see p. 135.

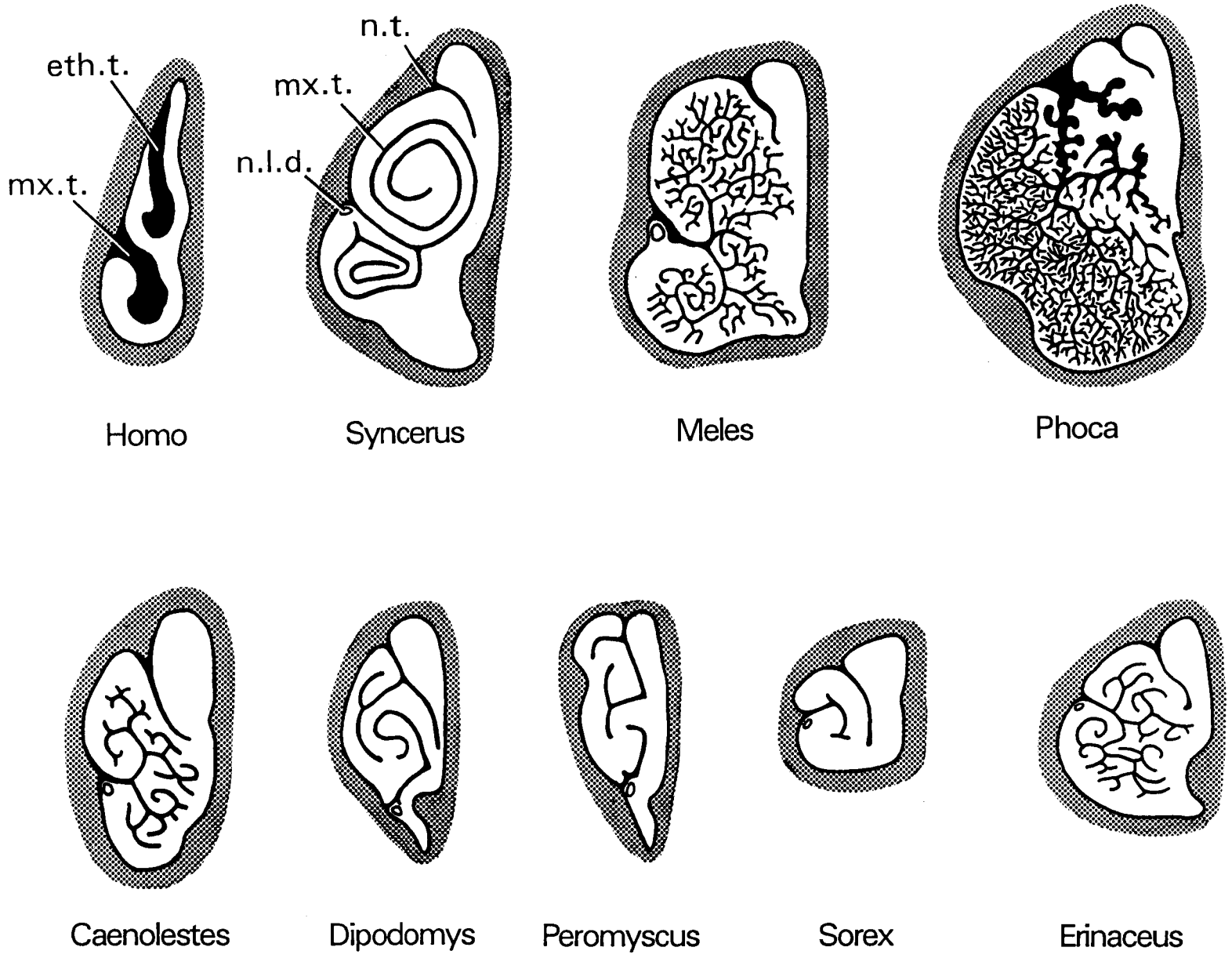

eth.t.
mx.t.
n.t.
mx.t.
n.l.d.
Homo
Syncerus
Meles
Phoca
Caenolestes
Dipodomys
Peromyscus
Sorex
Erinaceus

Figure 10. Path of respiratory air through the nasal cavity of the rabbit (Oryctolagus). Density of stippling indicates the relative volume of air conducted during ventilation (after Lucas and Douglas 1934). For abbreviations, see p. 135.

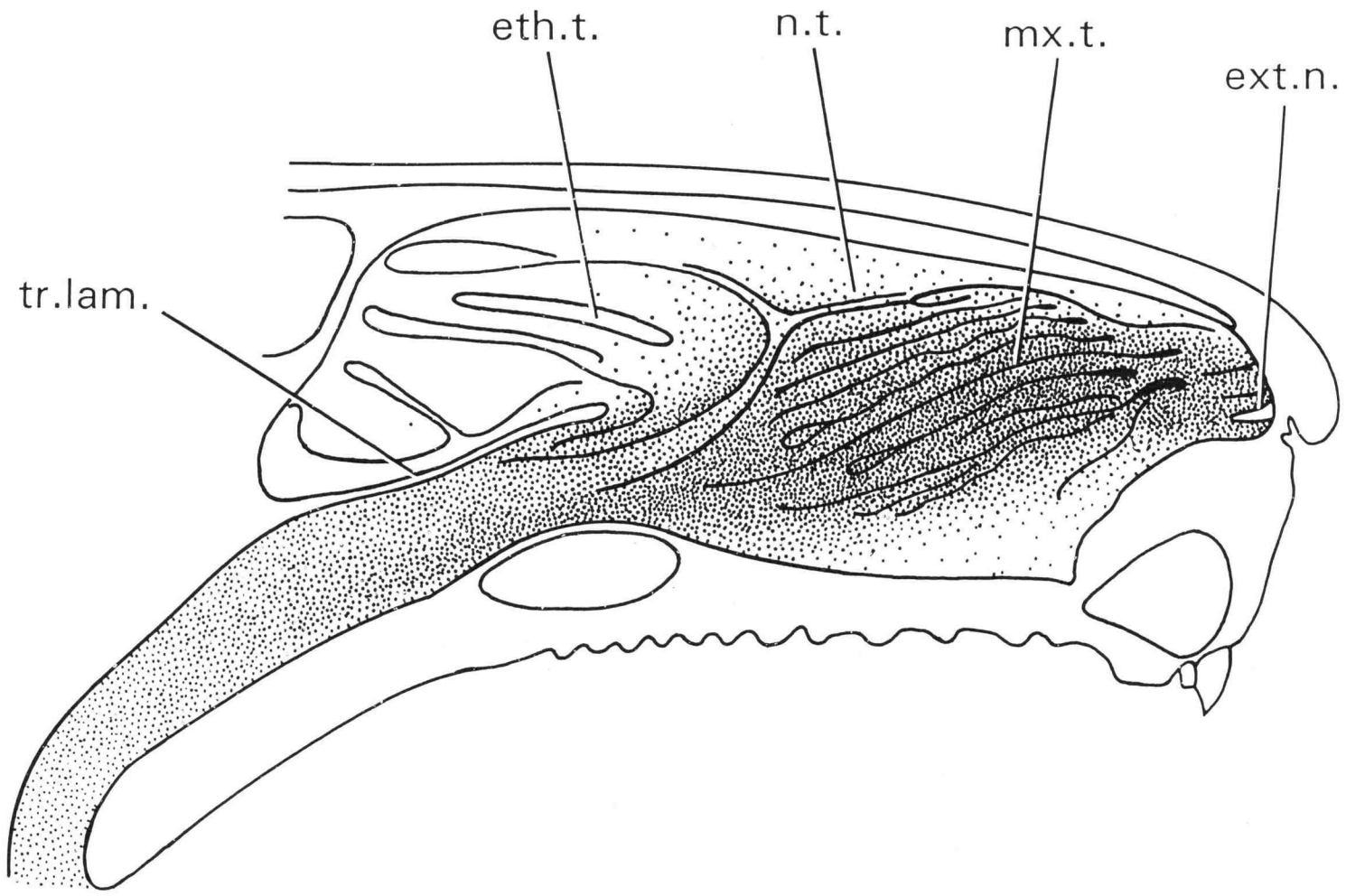

eth.t.
n.t.
mx.t.
ext.n.
tr.lam.

Figure 11. Stratigraphic ranges of the main groups of mammal-like reptiles (after Carroll 1988; phylogenetic relationships after Hopson and Barghusen 1986).

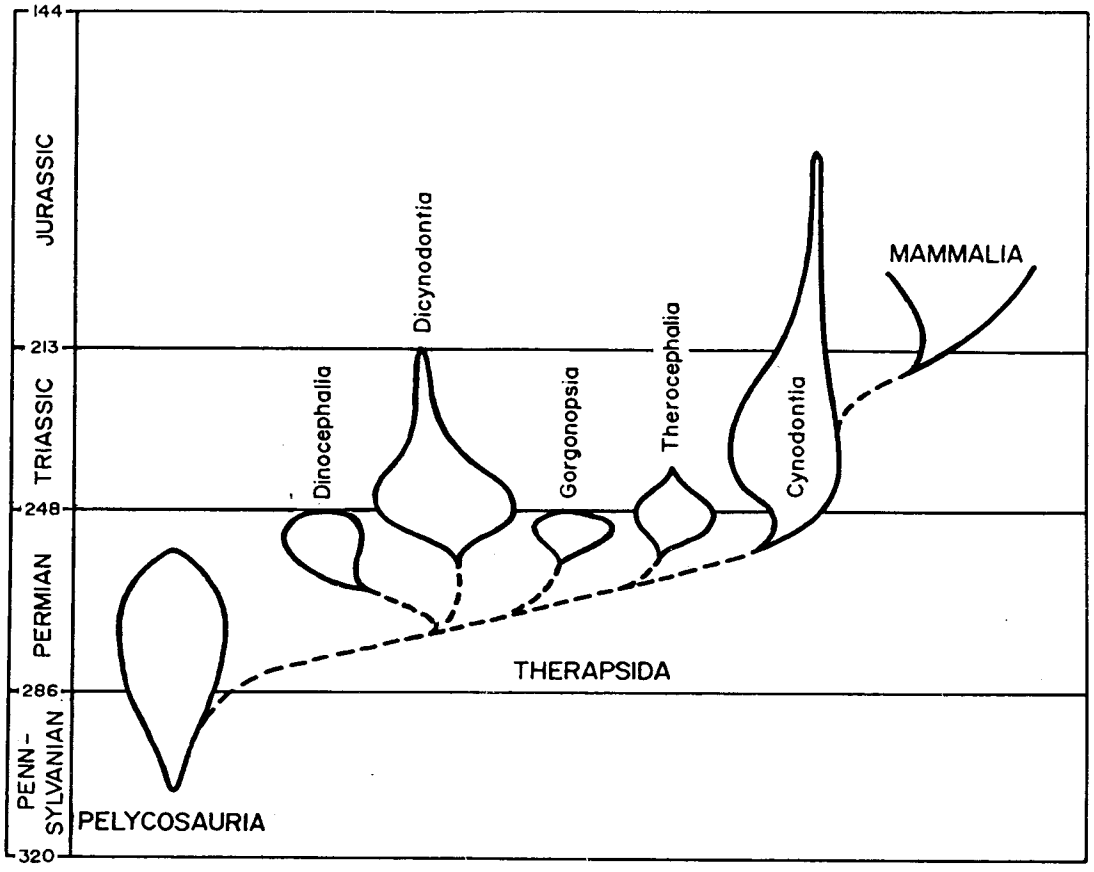

144
JURASSIC
213
TRIASSIC
248
PERMIAN
286
PENN-
SYLVANIAN
320
Dicynodontia
MAMMALIA
Dinocephalia
Gorgonopsia
Therocephalia
Cynodontia
THERAPSIDA
PELYCOSAURIA

Figure 12. The Pelycosaur nasal cavity. Dimetrodon, right sagittal section (modified from Romer and Price 1940). The position of the sphenethmoid bone is indicated by the dashed line. Scale bar is 1 cm. For abbreviations, see p. 135.

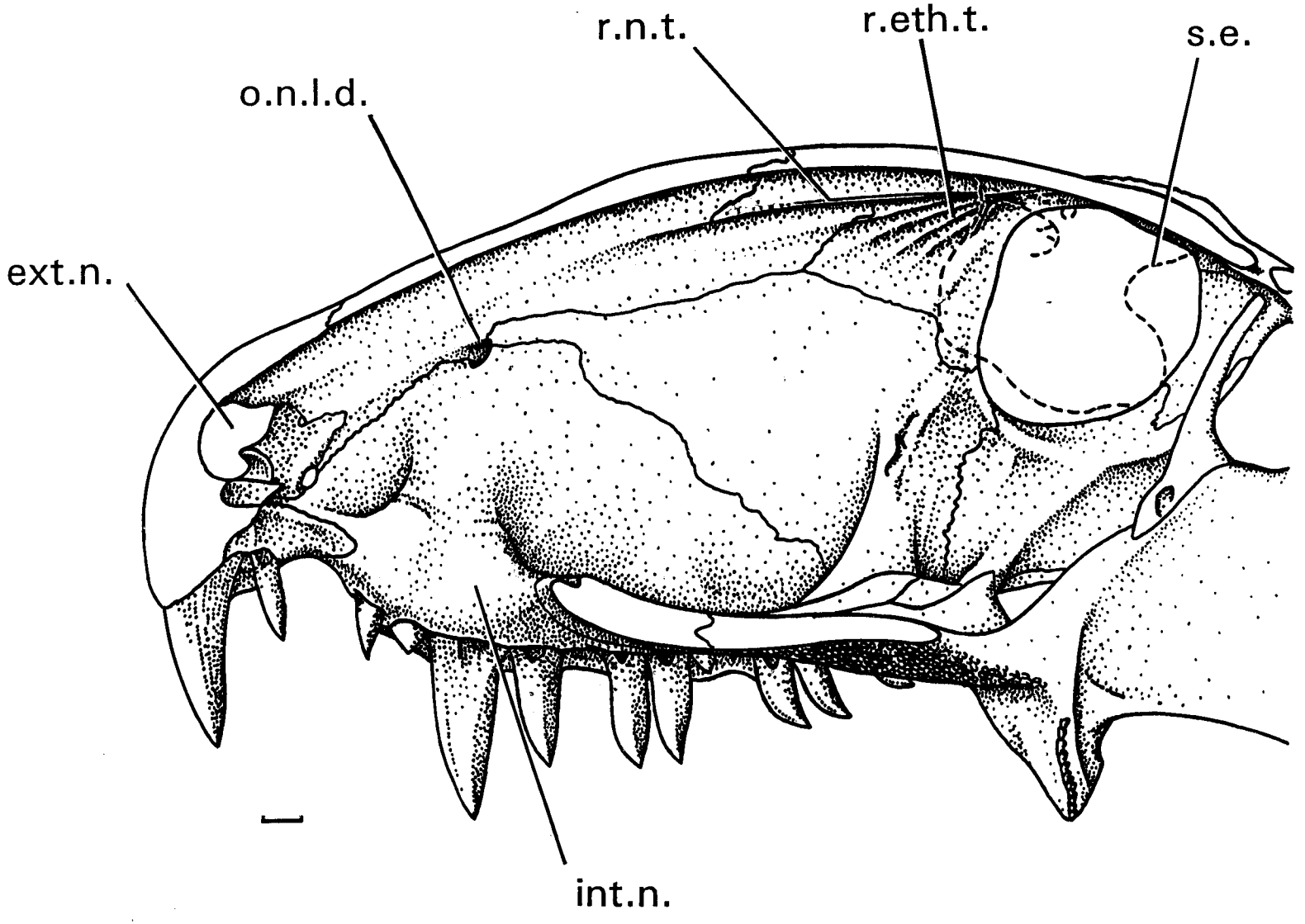

r.n.t.
r.eth.t.
s.e.
o.n.l.d.
ext.n.
int.n.

Figure 13. The dicynodont nasal cavity. Lystrosaurus, right sagittal section (modified from Cluver 1971). For abbreviations, see p. 135.

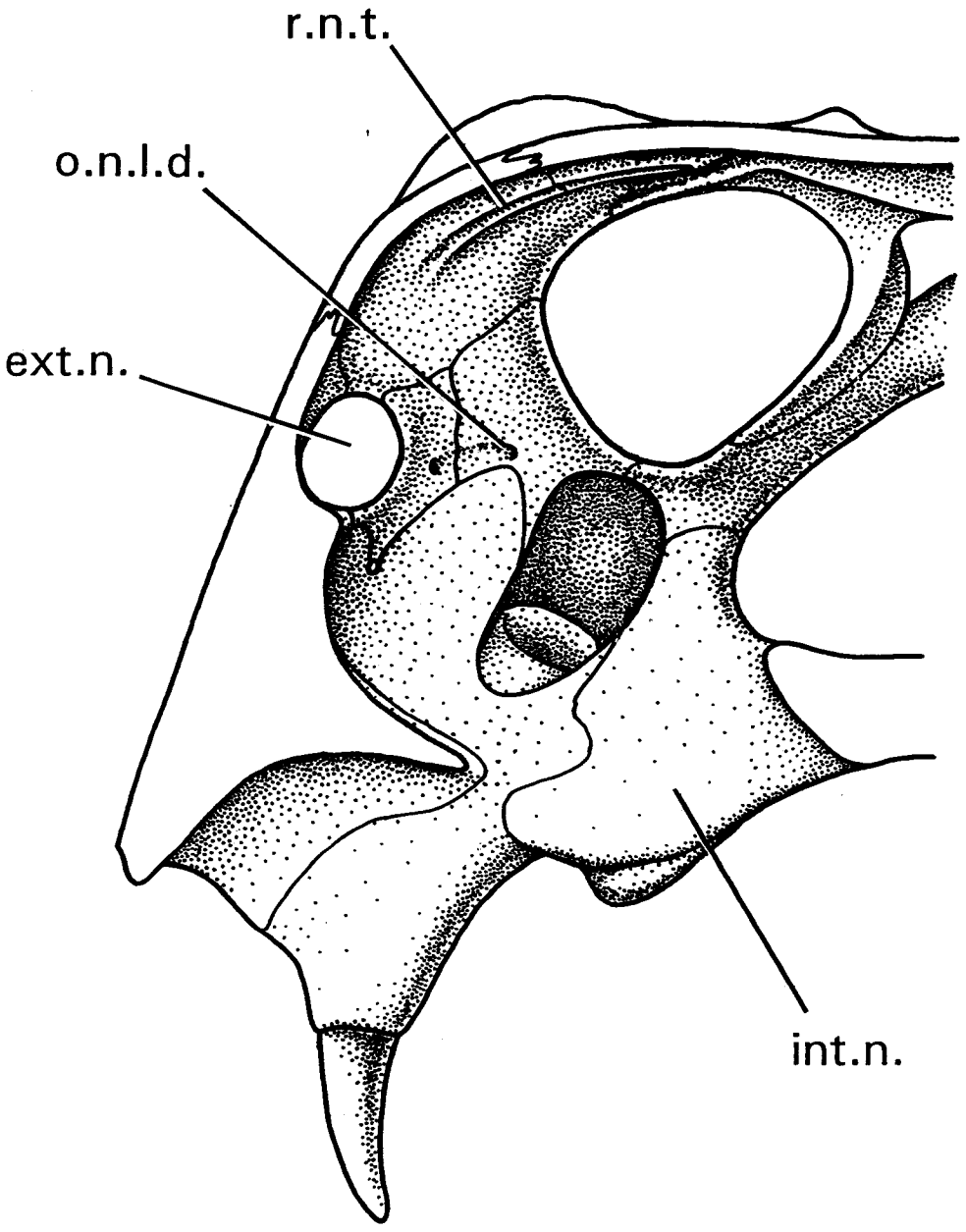

r.n.t.
o.n.l.d.
ext.n.
int.n.

Figure 14. Ventral view of the roof of the gorgonopsian nasal cavity. Based on Leontocephalus (modified from Kemp 1969). For abbreviations, see p. 135.

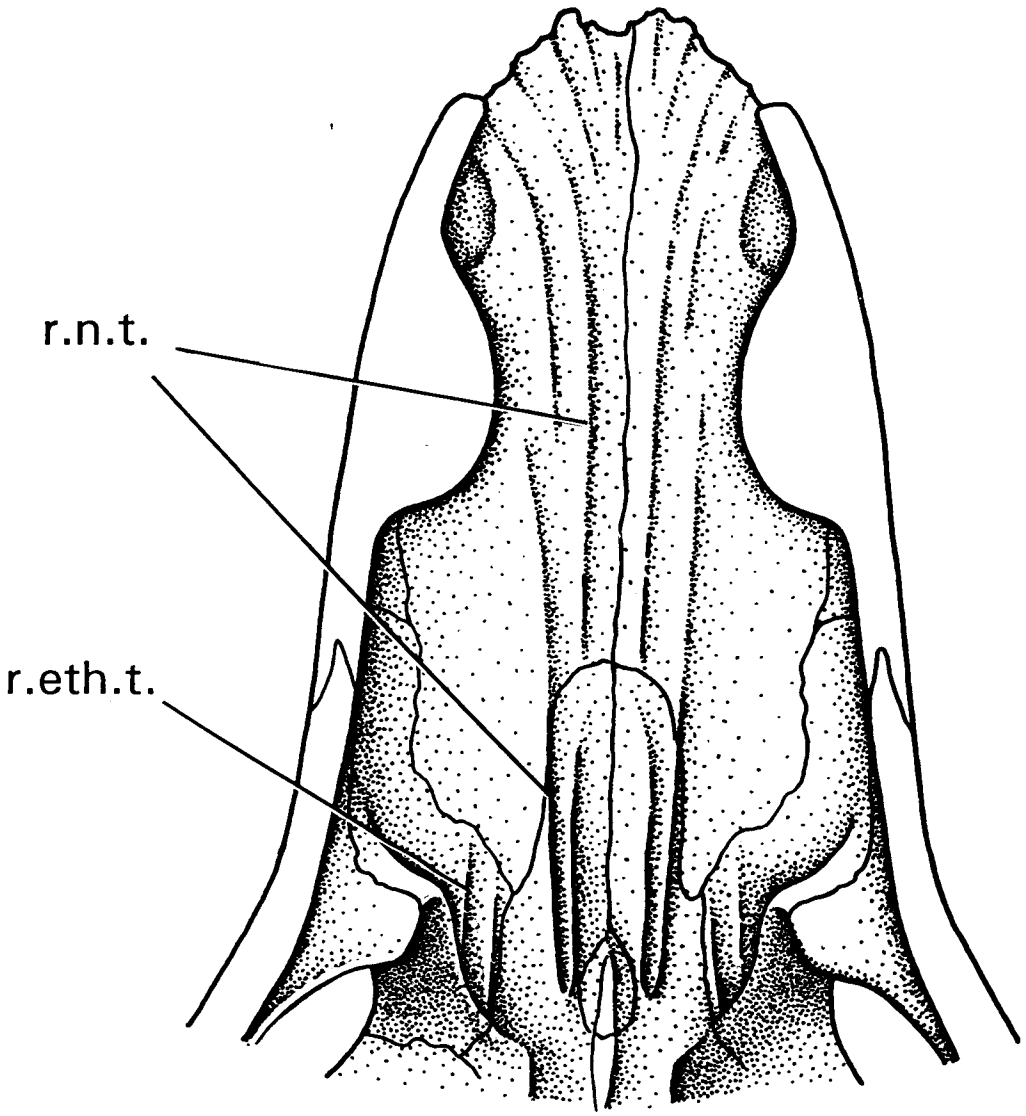

r.n.t.
r.eth.t.

Figure 15. The therocephalian nasal cavity. Glanosuchus, GS M796, right sagittal section. Scale bar is 1 cm. For abbreviations, see p. 135.

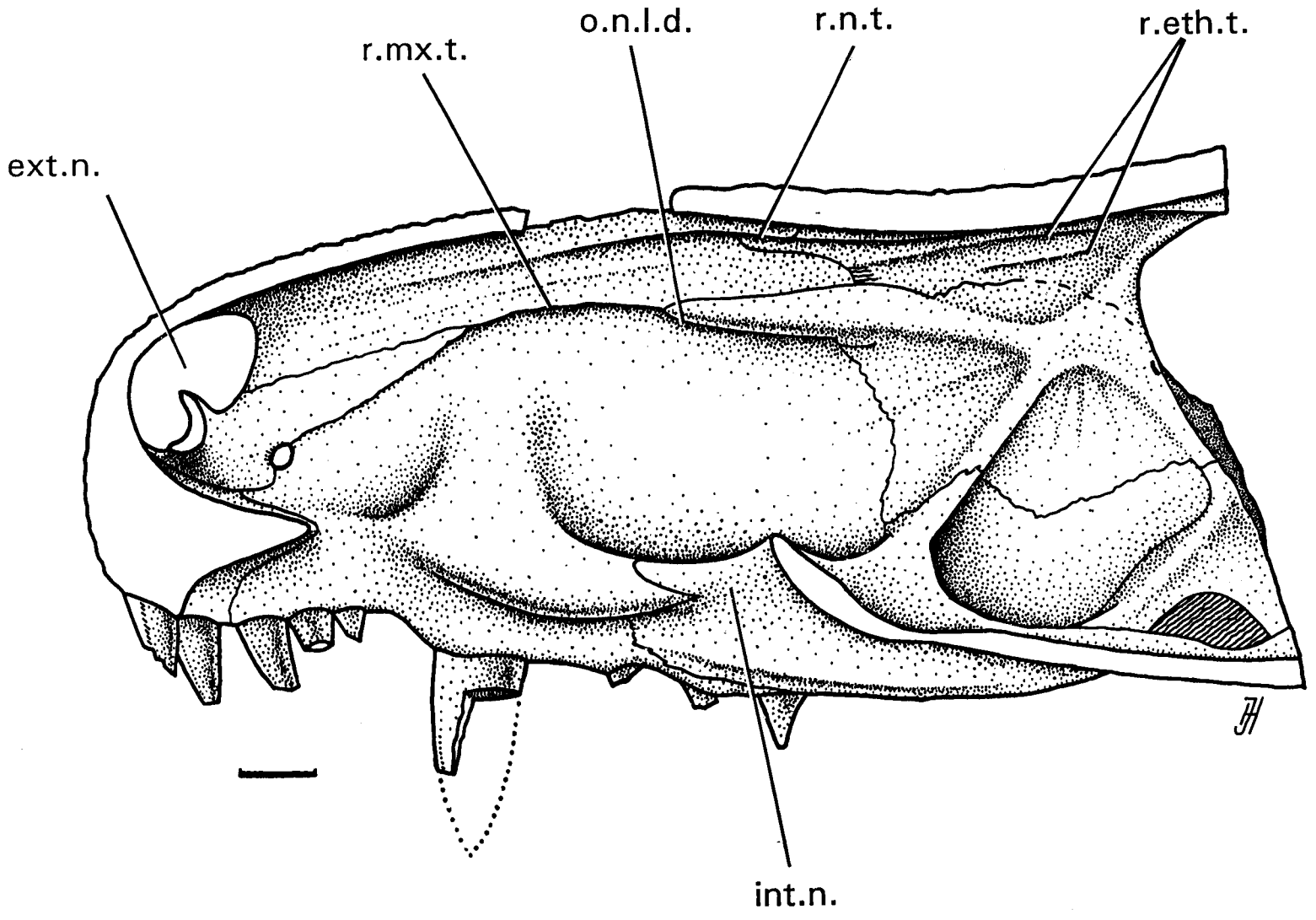
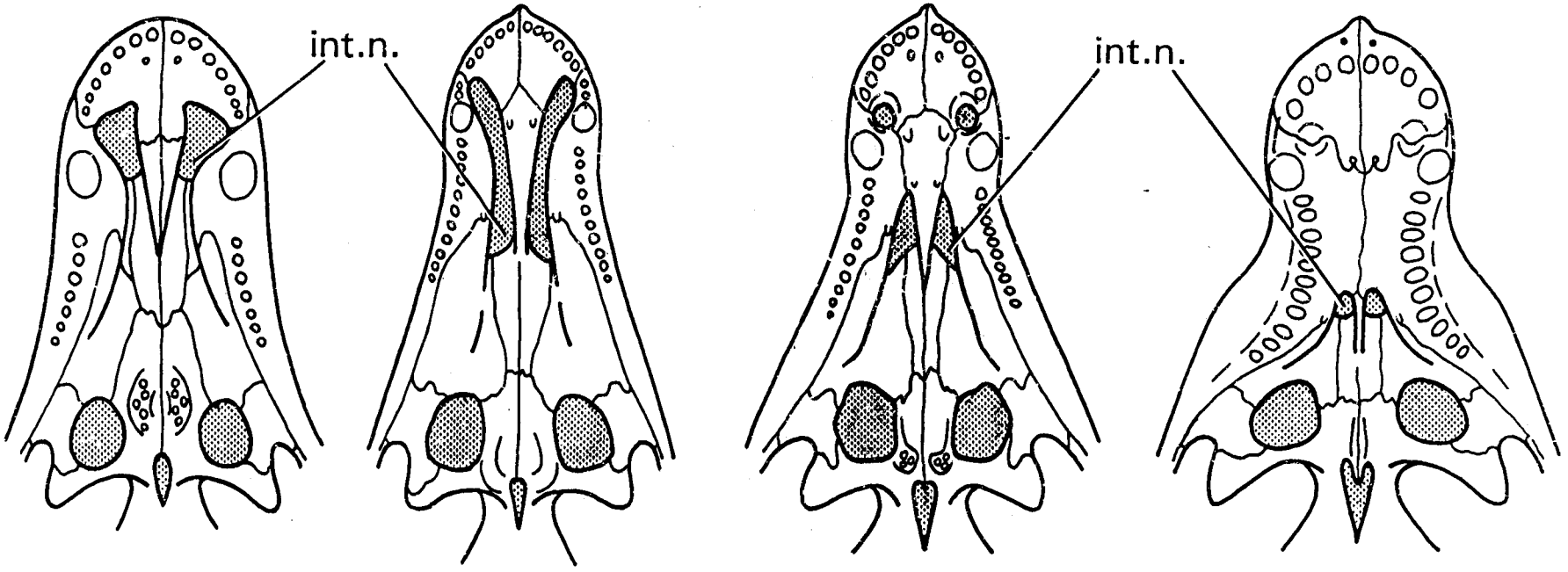

ext.n.
r.mx.t.
o.n.l.d.
r.n.t.
r.eth.t.
int.n.

Figure 16. The evolution of the therocephalian palate. Diagrammatic representation of the palates of several therocephalians, reduced to a common size, showing the posterior migration of the internal nares over time (after Mendrez 1975; the posterior portion of the palate of Pristerognathus based on Scylacosaurus, after Romer 1956). For abbreviations, see p. 135.



260 m.y. 250 m.y. 247 m.y. 244 m.y.

Pristerognathus Ictidosuchoides Regisaurus Bauria

Figure 17. Cross-section through the nasal cavity of the cynodont Massetognathus, MCZ 4240. The approximate location of the section is indicated in Fig 18. For abbreviations, see p. 135.

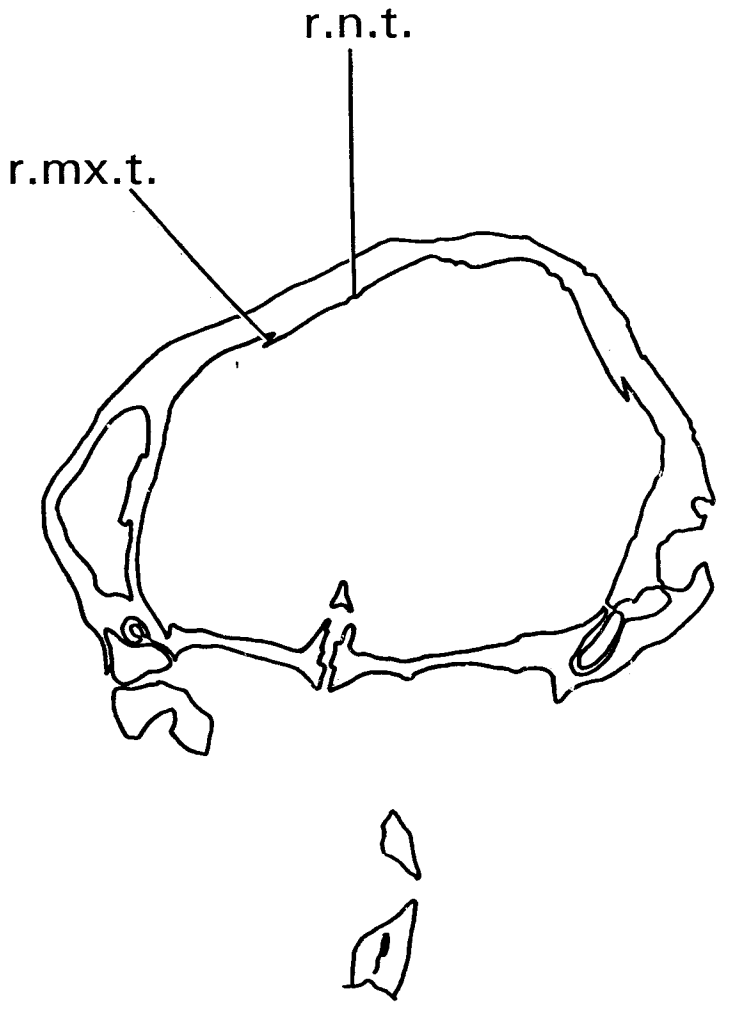
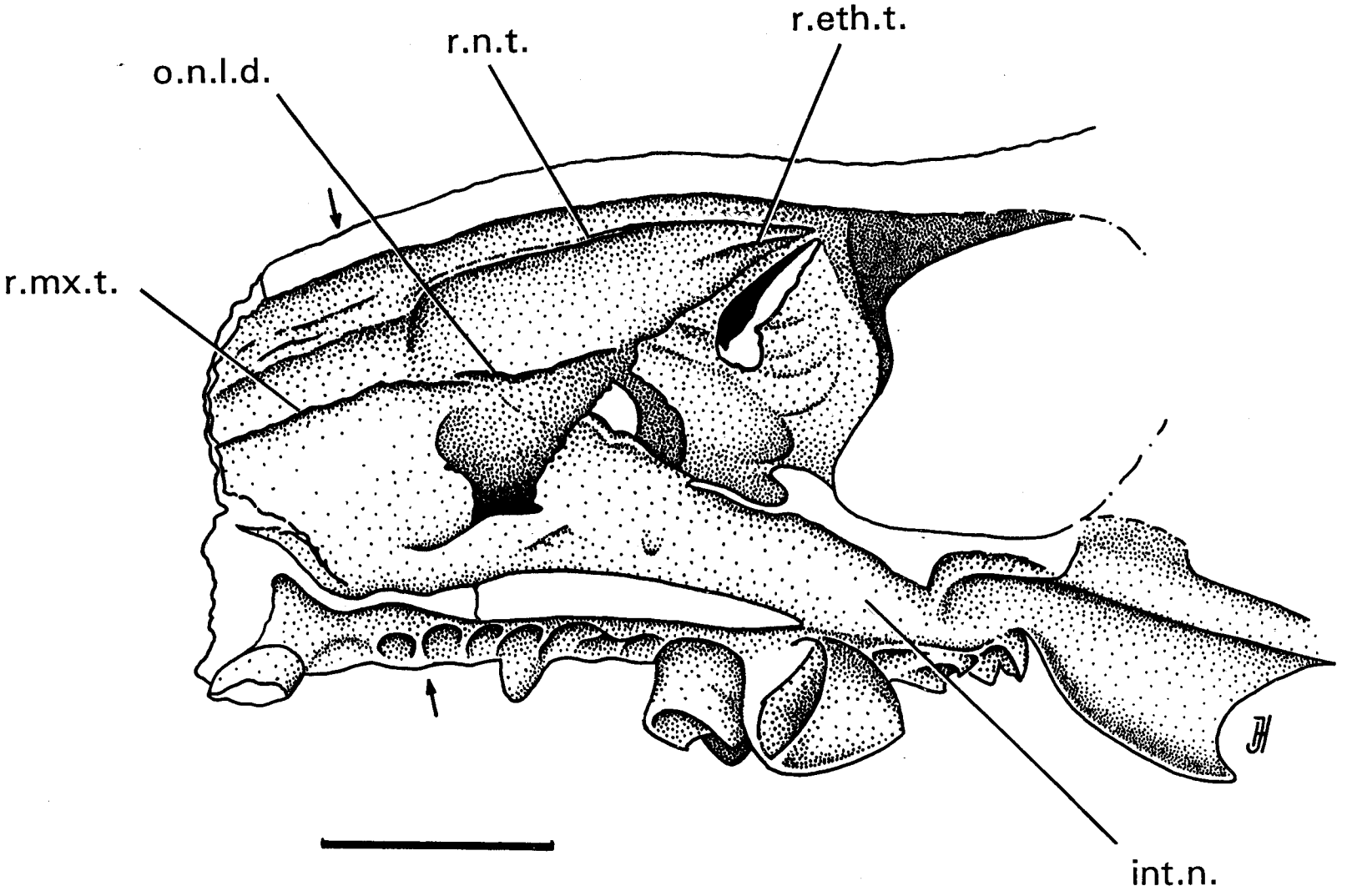

r.n.t.
r.mx.t.

Figure 18. The cynodont nasal cavity. Massetognathus, MCZ 4219, right sagittal section. Arrows indicate the approximate level of the section of Fig 12. Scale bar is 1 cm. For abbreviations, see p. 135.


r.eth.t.
r.n.t.
o.n.l.d.
r.mx.t.
int.n.

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APPENDICES

APPENDIX A

ABBREVIATIONS

SPECIMEN INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
GS	Geological Survey, Pretoria, R.S.A.
MCZ	Museum of Comparative Zoology, Harvard Univ.
NM	National Museum, Bloemfontein, R.S.A.
SAM	South African Museum, Cape Town, R.S.A.

ANATOMICAL ABBREVIATIONS

a.c.	anterior concha
a.t.	anterior turbinal
c.	concha
eth.t.	ethmoturbinal
ext.n.	external naris
int.n	internal naris
m.c.	middle concha
m.t.	middle turbinal
mx.t.	maxilloturbinal
n.l.d.	nasolacrimal duct
n.t.	nasoturbinal
o.n.l.d.	ostium of the nasolacrimal duct
p.c.	posterior concha

p.t.	posterior turbinal
s.e.	sphenethmoid bone
r.eth.t.	ridge for the ethmoturbinal
r.mxt.t.	ridge for the maxilloturbinal
r.n.t.	ridge for the nasoturbinal
tr.lam.	transverse lamina

APPENDIX B

LIST OF THERAPSID SPECIMENS WITH RIDGES FOR RESPIRATORY TURBINALS, DESCRIBED IN THIS THESIS

GS M796	Glanosuchus macrops (Therocephalia, Pristerognathidae)
AMNH 2226	Thrinaxodon liorhinus (Cynodontia, Thrinaxodontidae)
MCZ (uncat.)	Thrinaxodon liorhinus (Cynodontia, Thrinaxodontidae)
NMB QR3268	Trirachodon sp. (Cynodontia, Trirachodontidae)
MCZ 4219	Massetognathus pascuali (Cynodontia, Traversodontidae)
MCZ 4240	Massetognathus pascuali (Cynodontia, Traversodontidae)

APPENDIX C

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DEPARTMENT OF
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29 June
~~19 May~~, 1992,

Dr. D.L. Wolberg, Secretary
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of Mining and Technology
Socorro NM 87801

Dear Dr. Wolberg,

I just realised I sent you a fax without a return address. This explains why there was no answer previously. My apologies for this stupidity. Let me try again.

My manuscript, "The evolution of nasal turbinates and mammalian endothermy" was published in a recent issue of Paleobiology (vol. 18(1), 1992, pp. 17-29), to which the Paleontological Society holds copyrights. This article represents a major portion of my Ph.D. thesis research, which I plan to defend in several weeks.

I request permission from the Paleontological Society to use this article as part of my doctoral dissertation, to be submitted to Oregon State University. Please send me a notice granting permission by June 30, 1992, if possible. If you need additional information, please contact me.

Sincerely,

Redacted for privacy

Willem J. Hillenius

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